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## MODIFIED HYPHAE OF HYMENOMYCETES

PAUL L. LENTZ

*Division of Mycology and Disease Survey, Bureau of Plant Industry,  
Soils, and Agricultural Engineering*

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### INTRODUCTION

A study of Hymenomycete morphology can not fail to impress one with the variety of sterile hyphal ends found in the hymenium. In most mycological textbooks the basidiomycetous hymenium has been portrayed as consisting of basidia, "paraphyses" \* and perhaps a few cystidia. While this is essentially the case in many species, a vast array of Hymenomycetes exhibit all kinds of unusual hyphal modifications. These modified hyphal elements are not necessarily restricted to the hymenium; they may also be found at other surfaces of the basidiocarp and often within the context or trama. The discovery of structures such as these among the Hymenomycetes

\* The term "paraphysis" is a misnomer in the Basidiomycetes although correctly applied to some structures in the Ascomycetes.

has initiated a vigorous evolution in the taxonomic study of this group. In the modern classification of the Homobasidiomycetes, hyphal elements such as cystidia, setae and bizarre dendroid structures are criteria of genera and species. A careful appraisal must therefore be given such elements in any taxonomic study of the Basidiomycetes.

The nature of the modified hyphal elements of the hymenomycetous basidiocarp has been investigated over a period of more than 200 years. Micheli (1729) appears to have been the first mycologist to call attention to structures now known as "cystidia". He was also the first of many who attempted to formulate a possible justification for their existence, namely, that they might hold the lamellae apart in order that the spores may be freed. It is of interest to note that Buller, during the present century, advocated the same theory in relation to various species of *Coprinus*. Following Micheli, these elements were studied by several others, and the knowledge acquired from their work as well as from his own investigations was summarized by Corda in 1834. Another early naturalist, Hedwig (1789), apparently was the first person to use the term "paraphysis" in relation to fungi. As Boudier (1890) has indicated, Hedwig used that word to designate sterile filaments accompanying the endospore-bearing cells which he termed "thecae". The latter term had been used by Hedwig to denote the capsule of mosses; then he used it for asci of lichens and finally for asci of some Discomycetes which he placed in the genus *Octospora*. It is in relation to sterile filiform hyphae accompanying the thecae in *Octospora* that the term "paraphyses" first was applied. Fries (1821, 1822-1823) used the designation "ascus" for the sporiferous cells of both Ascomycetes and Basidiomycetes, for at that time the Basidiomycetes were believed to bear their spores endogenously. Léveillé (1837) recognized the necessity for revising the nomenclature of hymenial structures in the Ascomycetes and Basidiomycetes, and proposed the name "basidium" for that structure present in the basidiomycetous sporocarp while retaining Hedwig's term "theca" for that of the Ascomycetes. He also proposed the name "cystidium" to include those enlarged, conical or prismatic, translucent bodies which Micheli first had observed protruding beyond the hymenial surface. Persoon (1801, pp. X-XI) already had designated by the term "hymenium" the fertile surface



composed of thecae and paraphyses in the Helvellales, and this term was utilized by Fries in the first class of his "Systema Mycologicum" (1821, p. 1), class Hymenomycetes, of which *Agaricus* is the first genus.

In the meantime there was much conjecture about the attributes of cystidia. As mentioned, Micheli thought they were props to assist the escape of the spores from between the gills. L  veill   (1837) ridiculed this opinion, saying that Micheli attributed to Nature a remarkable prevision which would permit her to know that the cystidial props must be present so that the spores may escape. A much more reasonable theory seemed that expressed by Bulliard (1791, p. 39 ff.) who visualized the cystidia as the male elements. This belief was held also by Montagne (1842, p. 240) who discussed the "antheres" (cystidia) and said they seemed to represent fecundating organs. In 1875 W. G. Smith wrote that he considered the basidia to be female organs and the cystidia male organs, while the spores were probably unfecundated naked ovules without an embryo. "The spores fall to the earth and with them the cystidia, and it is upon the moist earth that fertilization is carried out". In 1881 he presented illustrations of various cystidia showing granular matter which he appears to have considered the fecundating agent. With the accumulation of evidence concerning the true nature of reproduction in the Basidiomycetes such ideas slowly disappeared, but modifications of them continued to be presented for some time. Massee (1887), for instance, thought cystidia were the terminations of laticiferous vessels and that their contents were poured out to supply a certain amount of food to the developing spores.

The laticiferous vessels of plants had been recognized first by Schultz (1822). His work was reviewed in 1837 by Saint-Hilaire who used the term "veines jaunes" in referring to laticiferous hyphae of *Lactarius deliciosus* (Fries) S. F. Gray. They were discussed by Corda (1839, p. 42; 1840, p. 49) and by Bonorden (1851, p. 188) who first distinguished sap vessels in general from the latex vessels of *Lactarius*. After the discovery of vessels many mycologists expressed the belief that cystidia were the hymenial terminations of these structures. De Bary (1873) noted that cystidia often arise from deep beneath the subhymenial region and give the appearance of being branches of laticiferous tubes, although he

was not able to see them originate from the latter. Bambeke (1892a, 1892b, 1892c, 1894, 1895) studied the vascular hyphae of various agarics. He considered them to be conducting hyphae, with their terminal ends in the stipe and lamellae often having the form of cystidia and functioning as excretory organs. Istvanffi and Johan-Olsen (1887) and Istvanffi (1896a, 1896b) published a classification of latex-containers and similar forms in their studies of the hyphal systems. They recognized laticifers, oleiferous organs, organs containing colored materials and materials becoming colored upon contact with air, and organs producing resinous materials. Oehm (1931a), studying the sap hyphae of *Lentinus squamosus* Quél. [= *L. lepideus* (Fries) Fries], came to the conclusion that such hyphae are less important as conducting elements than Istvanffi, Bambeke and others have believed. His reasoning is based upon the fact that such elements appear to be lacking from many regions where the conduction of materials would seem to be of greatest necessity, as in rapidly growing regions.

Certain cystidium-like structures are seen to originate from about the same level as the basidia and very obviously to be connected in no way with lacticiferous tubes. De Seynes (1873) suggested that these must be regarded as basidia returned to vegetative functions by hypertrophy. In other words, he considered the hymenium to be composed essentially of one organ, the basidium, but to form "paraphyses" when growth is arrested and cystidia if the basidium becomes greatly enlarged without producing spores. This concept of the nature of cystidia has been accepted rather generally in one form or another. Sometimes it includes the belief of Boudier (1890) and others that "paraphyses" merely represent immature basidia, although the theory of de Seynes implies that "paraphyses" are potentially basidia, but with their nature altered for some reason, instead of being merely young basidia which as yet do not bear spores. Because of his belief that "paraphyses" represent young basidia in the Basidiomycetes, Boudier considered use of the term "paraphysis" legitimate only when applied to Ascomycetes. In *Coprinus* Heinrich Lohwag (1926) found that the hymenial cystidia, basidia and "paraphyses" all are borne on the basidial fascicle, the cystidia being borne as elements of the first order (first and thus farthest developed in regard to size), basidia as elements of the second order, and "paraphyses" as elements of the third order.



Corner (1947) has expressed a similar opinion in relation to several species of *Clavaria* and *Oudemansiella*, suggesting that cystidia develop very much in the same way as basidia, but, failing to produce spores, become overgrown. Because of their homology with basidia, Corner expressed the belief that such cystidia could be substituted for the latter in calculating certain mathematical expressions of fungus morphology.

Maire (1902, p. 153), studying *Stropharia semiglobata* (Fries) Quél., and Kühner (1925), studying *Mycena fellea* Lange [= *M. erubescens* Höhn.], recognized nuclear fusion in cystidia and concluded that they represent basidia in which an abundant secretion has resulted in the arresting of normal development. Heim (1931, p. 43) says that, physiologically, cystidia and cystidiform hairs often have a tendency toward a role of excretion and that the origin of these organs is not necessarily always the same. Knoll (1912) regarded cystidia as trichome-hydathodes and presented numerous illustrations of such hydathode activity.

Patouillard (1881) called attention to the production of spores from hairs of the cap surface of *Pleurotus ostreatus* (Fries) Kummer and later (1889) reported the appearance of sporiferous regions on the superior surface of *Polyporus fulvus* Fries [= *Fomes fulvus* (Fries) Gill.] and *Polyporus nigricans* Fries [= *Fomes nigricans* (Fries) Gill.], on which spores were borne at the tips of hairlike structures. There were also various forms of sterile hairs. Patouillard claimed to recognize a complete homology between sporiferous hairs and normal basidia, sterile hairs and "paraphyses", colored hairs and cystidia. He believed that this gave evidence of the qualitative equality of all the filaments of a fungus, all potentially being capable of terminating as basidia, although many fail to do so because of the influence of various factors.

Boudier (1886) believed that cystidia should be regarded as sterile branches of the subhymenial tissue and should not be confused with sterile hairs, which might be found also in the hymenium, or with laticiferous vessels, which sometimes penetrate the hymenium. De Bary (1873), on the other hand, regarded cystidia as hairlike structures, a view similar to that adopted by Buller in the first four volumes of his "Researches on Fungi" (1909, 1922, 1924, 1931). In this compendium of his investigations, Buller discussed the structure and possible functions of "paraphyses" and

cystidia in several genera, including species of *Coprinus*, *Psathyrella* and *Lepiota*. He concluded that in some species "paraphyses" may be packing elements which help maintain the turgidity of the hymenium, while cystidia may act as stays to maintain the distance from one another of broad delicate lamellae. Recognizing the necessity of being able to designate cystidia by the area of the fungus on which they occur, Buller (1922, p. 324; 1924, pp. 52-53) introduced the terms "pleurocystidium", "cheilocystidium", "pilocystidium" and "caulocystidium" for those growing from the gill faces, gill edge, cap surface and stipe surface, respectively.

At this point it should be mentioned that not all cystidia and cystidium-like structures grow outward from the external surfaces of the sporocarp. For example, Overholts (1917) discussed the embedded setae in *Polyporus glomeratus* Peck. These setae, embedded in the trama of the pore walls, are large, brown, thick-walled tubes with tapered apices. Such structures seem to be characteristic for a number of polypores having a colored trama. *Pluteus admirabilis* (Peck) Peck has internally oriented elements which were regarded by Walker (1919) as internal cystidia. They are enlarged cells which appear to arise from the subhymenial layer and to grow diagonally inward toward the center of the trama.

As information was gradually acquired concerning modified hyphal elements, it became apparent that certain forms of these were associated so constantly with various species and genera of fungi as to constitute valuable criteria of taxonomic relationships. In the Thelephoraceae, for example, the genus *Hymenochaete* was proposed by L  veill   (1846) to include those species having setae. Actually he appears not to have distinguished between species bearing setae and those having cystidia. According to Wakefield (1914), Berkeley was the first to restrict *Hymenochaete* to the species having colored setae. Cooke (1879) proposed the genus *Peniophora*, to be distinguished from *Corticium* by the possession of metuloids (incrusted cystidia), and also suggested the possibility of delimiting, as *Veluticeps*, those forms of "*Hymenochaete*" having pointed tufts of slender septate hyphae passing from the subhymenium through the hymenium without bearing basidia. Distinctive modified elements have been useful in the taxonomy of other families as well. Many species of *Inocybe* have cystidia and so-called cystidiform hairs, and these have been utilized extensively



in the taxonomy of the genus since Karsten (1889, pp. 205-212) found that certain species could be characterized on this basis. Heim (1931, pp. 112-114), however, believes that the value of such structures has been overemphasized and advocates broadening the limits of species in this genus. An examination of the keys and illustrations of Smith's "North American Species of *Mycena*" (1947) will reveal the tremendous taxonomic importance of cystidiiform structures in that genus. Other recent works, in which modified hyphal elements are used extensively to characterize genera and species, include "The Agaricales (Mushrooms) in Modern Taxonomy" (Singer, 1951) and "A Monograph of *Clavaria* and Allied Genera" (Corner, 1950).

In the Thelephoraceae, pioneer work involving the consistent use of spores and cystidia as characters of taxonomic importance was done by Masee (1889, 1890). Burt (1914-26) adopted refined methods of microscopic study and was able to introduce uniform values into the classification of this family by the extensive presentation of modified hyphal elements in his keys and descriptions. In 1929 Overholts published a review of methods used in the taxonomic study of Basidiomycetes and described the modified hyphal elements which may be met, including cystidia, setae, gloecystidia, conducting cells, "paraphyses", vesicular bodies and hyphal pegs. His terminology and interpretation of these elements was essentially that of Burt. Bourdot and Galzin (1928), in their classical "*Hyménomycètes de France*", have reviewed these fungi in a comprehensive manner. Their terminology and interpretation of the differentiated hyphal elements took into consideration much of the knowledge concerning these structures and is to be preferred to that of Burt.

There are at least two excellent compendia which include a great amount of information concerning modified hyphal elements. Heinrich Lohwag's "*Anatomie der Asco- und Basidiomyceten*" (1941) must be consulted by one desiring knowledge of the vast literature dealing with the morphology of the higher fungi. Langeron's "*Précis de Mycologie*" (1945) is somewhat more readable and certainly more accessible than Lohwag's work. In addition to a discussion of cystidia, vascular hyphae and other such elements, it has a section on stains and staining techniques which can be very useful in the study of modified hyphal elements. A revised edition

of Langeron's work has appeared recently (1952). Finally, there are two papers which may be useful in a study of the chemistry of these elements. The first of these is Pastac's (1942) summarization of the chemical nature of colored materials which occur in the fungi. The other is Ulrich's (1943) review of the literature concerning the nature of chemical constituents of fungus cell walls, and including a discussion of methods for demonstrating the presence of such substances.

#### VASCULAR HYPHAE

The vascular hyphae constitute a heterogeneous group of structures which usually differ from the less conspicuous tramal hyphae by their size and form, and often by their contents. The terminology used to denote the various kinds of these hyphae has been exceedingly variable and inconsistent. This has been partly the result of disagreement concerning their contents and structure. Doubtless many, if not most, of these elements have the form of vessels, but some may be septate. Oehm (1933), for example, reported septa and clamp connections in some of the sap hyphae of *Polyporus squamosus* Fries.

Bambeke's (1892a, 1892b, 1892c, 1894) term "vaathyphen" or "hyphes vasculaires" (vascular hyphae) includes both laticiferous and nonlaticiferous elements. He included under this general term the structures known by the following designations: "veines jaunes" (C. H. Schultz), "Lebenssaftgefäße" (Corda), "Saftgefäße" and "Milchgefäße" (Bonorden), "Milchsaftgefäße" (H. Hoffmann, de Bary, Weiss), "vaisseaux laticifères" (Boudier), "laticifères" (Patouillard), "réservoirs à suc propre" (de Seynes), "Milchsaft führendes Zellen" (Dippel), "laticiferous vessels" (Massee), "vaisseaux oléifères" and "vaisseaux laticifères" (Fayod), and "Milchsaftbehälter" (Istvanffi and Johan-Olsen).

Generally the various elements included under the terms of Bambeke and Oehm have been designated according to their contents; this has not always resulted in homologous usage. Fayod (1889), for example, held the view that *Russula* possesses only oil vessels, while *Lactarius* has both oil and latex vessels. Some mycologists now believe that latex-containing hyphae occur in both genera. In addition to latex, many other substances have been recognized in these various hyphae. Some of these are fats, resin-



ous materials, proteins, glycogen, dextrin, tannic acid, cyanic substances, colored materials and aromatic substances.

Istvanffi (1896*b*) grouped fungus hyphae into four systems: the meristem, the system of protection, the system of nourishment, and the system of propagation. The latex containers, fat containers and similar elements were placed in the system of nourishment as conducting elements. Istvanffi noted that the tubes may be either full or empty, and thought that the abundance of contents was in closest correlation with the development of the sporocarp. While most mycologists have considered the contents of the various kinds of sap hyphae to be nutritive substances and that these hyphae have the function of distributing such nutritive materials (Bambecke, 1894), Lohwag (1941, p. 384) has pointed out that they could function as excretory elements. However, he notes that these elements are a heterogeneous collection which have in common only the possession of dense, light-refractive, often slightly colored contents, and that sometimes the same kinds of contents appear in the hymenial elements or even in all the cells of the basidiocarp.

Oehm (1931*a*) studied the sap hyphae of *Lentinus squamosus* Quél. [= *L. lepideus* (Fries) Fries] and a related form, and enumerated certain qualities which these hyphae would be expected to have if they were really the primary conductors of nutritive substances in the basidiocarp:

(1) They should be most abundant in the parts of the fungus which serve especially for conduction (as an entire organ), such as rhizomorphs.

He classed as rhizomorph-forms the true rhizomorphs growing within the substratum, similar forms growing externally, and rhizomorph-like very long stipes. He found few sap hyphae in the true rhizomorphs and in the rhizomorph-like stipes, but many in the rhizomorphs growing free in the air.

(2) Sap hyphae should be distinguished from other hyphae by definite characteristics.

In some cases, notably *Lactarius*, the contents of sap hyphae were found to be distinctly different from those of the other hyphae of the same sporocarp, but this was by no means always true in other genera. Sap hyphae take their origin from the ordinary hyphae, and, at least in *Lentinus*, Oehm found that this may occur not only in the young mycelial stage but often even in the fully developed cap.

(3) Sap hyphae should be developed at least throughout the length of the stipe and into the midst of the cap flesh.

Oehm found that often there was not a continuous system in these parts.

(4) Sap hyphae should appear in the same parts of all the basidiocarps of the same species.

Oehm found that this was not the case.

(5) Sap hyphae should be most abundantly developed at the places of greatest necessity for nutriment, i.e., in the lamellae.

They often are abundant in these places in old sporocarps, but appear to be lacking in young fructifications, at least in *Lentinus squamosus* and *L. squamosus* f. *suffrutescens* (Fries) Oehm.

Summing up, Oehm came to the conclusion that the basic conducting elements in these forms are the ordinary hyphae, since only these appear under all the necessary conditions cited. The sap hyphae appear to originate from the ordinary hyphae either by enlargement at the growing apex as the lumen of the hypha becomes thickened below, or by swelling along the length of the ordinary hyphae. Thus he concluded that no primary distinction exists between ordinary hyphae and sap hyphae in these forms, but that the sap hyphae merely take over the functions of the ordinary hyphae and are then the conducting hyphae after the ordinary hyphae have lost most of their ability to carry on such functions as the result of narrowed lumina. Oehm (1933) found similar relationships between the sap hyphae and ordinary hyphae of *Polyporus squamosus* Fries. The contents of the thin-walled sap hyphae were not basically different from those of the ordinary hyphae, and the sap hyphae appeared not to have a greater part in conducting food materials than the other hyphae. According to Lohwag and Peringer (1937), the sap hyphae of the Boletaceae seem to arise from the connective hyphae which the authors consider to be the basic building hyphae of the sporocarp.

In so far as movement of water is concerned, the so-called vessels or vascular hyphae of fungi are not to be considered analogous to the vessels of higher plants. There are no elements in the basidiocarp comparable to tracheids or vessels. Pieschel (1924) studied water movement in a considerable number of agarics. By use of dilute stain solutions he found that conduction through the stipe and cap depends largely on capillary movement of water along the



minute spaces between the hyphae. In this way, some of the water may actually pass through the stipe and enter the cap without having passed through a single cell wall.

**LATICIFEROUS HYPHAE.** Laticiferous hyphae occur in several genera of the Hymenomycetes, but those of *Lactarius* and *Russula* are the most conspicuous and were recognized earlier than other kinds of vascular hyphae. In addition to *Lactarius*, the species in *Mycena* sect. *Lactipedes* and some in a few other genera, e.g., *Collybia*, and some of the Polyporaceae may have a true latex (Heim, 1942). Others may have a very scanty latex or may have laticiferous hyphae with the contents coloring but not containing a fluid latex; such may be found in *Russula*, in *Inocybe* sect. *Lactiferae*, and in *Entoloma lividum* (Fries) Quél. [= *Rhodophyllus lividus* (Fries) Quél.]. The true laticiferous hyphae are long tubes which are usually of greater diameter than the ordinary tramal hyphae. Those of some species of *Lactarius* have been reported to be about ten micra in diameter, but some may be as broad as 20 micra or more. Those of *Russula* usually are not so large. Kühner (1938, p. 44) found that the laticiferous hyphae in *Mycena* are of approximately the same size as the fundamental hyphae. They may be of uniform diameter or may have swellings at intervals. The longitudinal wall is thin and flexible. Cross walls usually are lacking or may be found only at considerable intervals from one another. Hallier (1866) reported occasional cross walls in laticiferous hyphae of *Lactarius pergamenus* (Fries) S. F. Gray. The tubes are undulating or sometimes variously bent and wound; often they are profusely branched. According to Bambeke (1892a, 1892b), they have a tendency to divide dichotomously. They undergo numerous anastomoses with one another, and also are in frequent union with ordinary hyphae of the trama.

Investigations have usually shown that latex hyphae may be found at a very early stage in the development of the sporocarp, before any differentiation of the latter has begun. Istvanffi and Johan-Olsen (1887) found that the latex hyphae originate as sprouts or outgrowths of the ordinary hyphae in the very earliest formative stages of the fruiting body. Originally they are not very numerous, but they increase in abundance by branching. Massee (1887) recognized two forms of latex containers in *Lactarius*. In *L. deliciosus* (Fries) S. F. Gray he found that the vessels are the

result of cell fusion, with only a few of the transverse septa remaining, while those in *L. torminosus* (Fries) S. F. Gray consisted from the first of much-branched aseptate hyphae. Weiss (1885) also reported that the tubes of *L. deliciosus* are formed as typical fusion structures, homologous in that respect with many latex vessels of the higher plants.

In the young basidiocarp the latex hyphae are distributed more or less equally in all parts. In older fruiting bodies there appears to be a specialization so that the tubes are most abundant in the peripheral region of the stipe and the subcortical region of the cap, as well as in the subhymenial region of the gills. In the latter they extend along in the subhymenial region parallel with the surface of the gills and eventually turn vertically to press between the basidia and end at the free surface of the hymenium. Istvanffi and Johan-Olsen (1887) have recognized two modes of distribution in the various species of *Lactarius*. In some the stipe possesses a simple cortex. In these the tubes are distributed in the cortex, extending in a direction parallel with the axis of the stipe and sending side branches to the central hyphal mass. In others, with a more complex cortical layer, there may be two layers of latex tubes separated by a thin layer of the cortex. In these forms the tubes of the inner layer send branches into the central hyphal mass.

There has been lack of agreement concerning the relationship of the laticiferous hyphae to the pseudoparenchymatic elements, most abundant in the stipe, known as "sphaerocysts". Although de Bary (1887, p. 299) believed that the thin-walled hyphae extending through the central axis of the sphaerocysts were not laticiferous tubes, both Hallier (1866) and Istvanffi and Johan-Olsen (1887) believed these hyphae had turbid contents and were laticiferous hyphae. Oehm (1931*b*) has established that the rosettes of sphaerocysts in *L. deliciosus* have an intercellular space at their axis in about one-third of the observed instances, while the others center around a laticiferous vessel. He found that the central laticiferous vessel may branch on occasion so that the larger central tube may be surrounded by several smaller tubes.

In *Lactarius*, *Mycena* and *Lentinellus* the latex hyphae have numerous nuclei which are dispersed in the cytoplasmic tube adjoining the wall. This multi-nucleate condition is typical of coenocytic elements and is noted in most types of vascular hyphae.



Kühner (1926) found the cytoplasm of the laticiferous hyphae of *Lactarius* to be in the form of a dense but delicate reticulum. In addition to the living cytoplasmic lining, the tubes of *Lactarius* contain an abundant latex in the form of a turbid emulsion of finely-granular droplets suspended in a liquid which, according to Massee (1887), is always whitish when in the unbroken tubes but usually assumes some other color upon contact with the air. It may then be white, pink, red, yellow, green, blue or some other color, the color change evidently resulting from some alteration occurring in the granular portion of the latex. According to Heim (1943), the latex of *L. melanogalus* Heim is black, while *Bertrandia astatogala* Heim (near *Hygrocybe*) has latex which undergoes color changes from cream to orange, lilac, gray-green and gray-black, and *Mycena atro-violacea* Heim has latex which is hyaline at first, then brownish, and finally blue-black. Color changes such as these are (Heim, 1942) facilitated by the action of oxidases, such as tyrosinase or other enzymes.

De Bary (1887, p. 299) found that the latex of *Lactarius* coagulates at the temperature of boiling water and when treated with alcohol. Boudier (1866, pp. 78-80) reported that the contents of laticiferous hyphae are rich in proteins and also contain a resinous material. Several others have found a resinous material in suspension in the tubes, while Bambeke (1892*a*, 1892*b*) reported the presence of glycogen. Arnould and Goris (1907) found that Ronceray's sulfovanillic reagent caused the laticiferous hyphae of *Lactarius* and *Russula* to turn blue, and Kühner (1926) wrote that those in *L. rufus* (Fries) Fries are recognizable by the black coloration which they generally assume when stained with hematoxylin.

**OLEIFEROUS (FAT-CONTAINING) HYPHAE.** Oleiferous hyphae are more widespread through the Hymenomycetes and more variable than the other kinds of hyphae with noteworthy contents. According to Kühner (1938, p. 43), oleiferous hyphae are more or less infrequent in the individual basidiocarp but are found in all agarics. Istvanffi and Johan-Olsen (1887) have grouped fat containers as long slender elements, short club-shaped elements, and globose elements. Although all of these may contain fats, in general only the long slender structures should be termed "oleiferous hyphae". The others are for the most part gloeocystidia.

There are many transitional forms between latex hyphae and

oleiferous hyphae, the major difference being that of content, not of form. Oleiferous hyphae are long tubes, rather slender, usually with thin walls and varying from much-branched, as in *Nyctalis*, to completely unbranched, as in *Ptychogaster* (Istvanffi and Johan-Olsen, 1887).

They extend in an undulating course among the ordinary tramal hyphae. In *Mycena*, Kühner (1938, p. 43) found that the oleiferous hyphae resemble in form and size the connective hyphae from which they are derived. It seems certain that their origin is very much like that of the latex hyphae, i.e., they arise evidently as branches or extensions of the ordinary hyphae, usually at an early stage in the development of the sporocarp. Their distribution in the basidiocarp is very much the same as that of the latex hyphae. In the cap-bearing fungi they are especially plentiful in the peripheral region of the stipe, in the crown of the cap and in the hymenium. In other Hymenomycetes, according to Istvanffi and Johan-Olsen (1887), they are distributed throughout the basidiocarp.

Like the latex hyphae, the oleiferous hyphae usually are considered to be coenocytic. Kühner (1938, p. 44) failed to find any nuclei in them. Generally, though, it has been reported that nuclei are distributed in the finely granulated protoplasmic tube lining the wall. Within the tube is a dense, sometimes scarcely fluid, refractile, homogeneous substance which often is considered to be of a fatty nature. Bambeke (1892*a*, 1892*b*, 1894) suggested that the composition of the contents of these hyphae must vary greatly in different fungi and that they may be termed "oleiferous hyphae" only in the most general sense. Kühner (1938, p. 44) also was of the opinion that fatty substances constitute a very small part of the contents of these hyphae. He (1925) found that the vascular hyphae of *Mycena fellea* Lange [= *M. erubescens* Höhn.], though they are filled with refractile globules, do not color with osmic acid and thus apparently are not of an oily nature. The oleiferous hyphae usually are considered to have some important physiological role, but what that is remains obscure.

Distinct from the oleiferous hyphae are those which bear ethereal oils. These are aromatic compounds which are recognized usually by their odor, sometimes by color changes which they undergo upon contact with air or various reagents. Ethereal oils are contained in



tubes which form a branched network similar to that of many latex hyphae. Ethereal oil hyphae occur in various species of *Flammula*, *Inocybe*, *Naucoria* and *Pholiota*, and Istvanffi and Johan-Olsen (1887) reported aromatic substances in vascular hyphae of *Trametes odorata* (Fries) Fries. Bambeke (1895) reported that the anise-like odor of *Lentinus cochleatus* Fries [= *Lentinellus cochleatus* (Fries) Karst.] is produced by an essential oil carried by the vascular hyphae of this species. Chemically, the ethereal oils are related to tannic acid, mentioned below, since both are aromatic compounds.

**SANGUINOLENTOUS HYPHAE.** Vascular hyphae with blood-colored contents occur in several species of *Stereum* and also in *Fistulina*. In some species, particularly in *Fistulina* (Oehm, 1931a), *Stereum rugosum* (Fries) Fries and *S. sanguinolentum* (Fries) Fries, the hymenial surface may ooze a dark red liquid when injured. In *S. gausapatum* (Fries) Fries and some other species the liquid is not so abundant, so that the injured hymenium merely becomes discolored. Other species of *Stereum*, particularly *S. fasciatum* (Schw.) Fries, *S. hirsutum* (Fries) S. F. Gray and a number of similar species, may have a few hyphae with dark red contents, but in these the hymenium does not discolor or bleed when injured. In all of these species there are thick-walled tubes apparently homologous with the sanguinolentous hyphae in structure but lacking colored contents.

Kindermann (1901) has made a detailed study of the sanguinolentous hyphae in a fungus which he thought was *Stereum sanguinolentum*. According to Höhnelt and Litschauer (1908, p. 60), Kindermann's fungus actually was *S. rugosum* and his observations apply to that species, not to *S. sanguinolentum*. Kindermann was in error also when he reported that the sanguinolentous hyphae in his fungus, *S. rugosum*, measure 39 to 52 micra in diameter. Calculations from his illustrations reveal that they are approximately seven to 15 micra in diameter. Those of *S. sanguinolentum* are mostly about eight to ten micra in diameter, very long, mostly unbranched, and with somewhat thickened, hyaline walls. Kindermann found that the walls of sanguinolentous hyphae in *S. rugosum* contain less chitin than those of the ordinary context hyphae. Cross walls may occur in some instances but apparently are rare. The tubes of *S. rugosum* show occasional pyriform swellings at

infrequent intervals, but for the most part they are of moderately even diameter along their length. The apex may be somewhat swollen, and the membrane becomes so thin in this region that there sometimes appears to be an apical opening.

Kindermann found that the sanguinolentous hyphae seem to originate from the ordinary context hyphae by chemical modification of their contents. He supports his opinion with two observations. The first of these is his failure to find many of these hyphae in the basal strata of the basidiocarp, thus leading him to the conclusion that they do not necessarily originate there. In addition he found, here and there, hyphae which completely resemble ordinary context hyphae toward their bases but which become filled with brownish contents farther along and then are typical sanguinolentous hyphae. These hyphae appear rather early in the formation of the basidiocarp.

The sanguinolentous hyphae are dispersed irregularly in the context and subhymenium. Usually they are most conspicuous in the subhymenium, whence they curve into the hymenium among the basidia. In older specimens their tips may protrude slightly beyond the hymenial surface. Typical sanguinolentous hyphae have contents which appear dark brown or reddish brown when seen through the microscope. When the liquid leaves the hypha, it becomes deep red; this is caused by oxidation, according to Kindermann. The contents of the hyphae consist of a homogeneous liquid in which float numerous clear or dark oily droplets. Tests with iron chloride and with potassium oxide convinced Kindermann that tannic acid is the principal constituent of the liquid portion; thus he used the term "Gerbstoffhyphen" (tannic acid hyphae) in referring to these structures.

Overholts (1929) surmised that the appearance of sanguinolentous hyphae under the microscope indicates that they are conducting cells or reservoirs for special types of liquid materials. According to Kindermann, the tips of the hyphae, protruding slightly beyond the hymenial surface, open up and empty their contents over the hymenium, thus moistening the basidiocarp and preventing it from rotting.

**HYPHAE WITH COLORED CONTENTS OR WITH CONTENTS COLORING IN AIR.** Many fungi have hyphae which contain colored materials, usually yellowish or brownish, in which the color is generally



associated with particles such as "fat" globules. There are others, however, which have the color or colorable material dissolved in a more or less thin fluid and not bound to solid or oily particles. Such fungi are especially prevalent among the species of *Boletus* and also are found in species of *Russula* and a few other genera.

The tubes containing these colored materials are very much like the latex hyphae, being long, rather slender, much-branched, and entering very abundantly into union with the other hyphae of the context. They appear in the stipe, cap and hymenium of the boletes, but are most abundant in the peripheral part of the stipe and also in the entire basal region of the stipe. In some boletes, according to Lohwag (1941, p. 403), contents of all sap hyphae can become colored upon contact with air; thus in these the sap hyphae lying near the periphery of the sporocarp are the ones which normally have colored contents. In *Boletus badius* Fries [= *Xerocomus badius* (Fries) Kühner ex Gilbert] Lohwag and Peringer (1937) found that the hyphae of the young trichoderm of the cap surface eventually change to sap- or pigment-containing hyphae.

The colored-material hyphae contain a watery liquid in which the colored material is dissolved, and the liquid is often as colorless as water before being exposed to the air. It is thought that the poisonous materials of some boletes may be contained in these tubes. In the red-pored boletes the wounded flesh colors blue quickly but gradually fades to a dull red. According to Bertrand (1933), the change of color of many boletes depends upon boletol which, under the influence of laccase, oxidizes to boletquinone which forms deep blue salts with ions of calcium, magnesium and potassium which are present. The reddening and subsequent blackening of the flesh of *Boletus strobilaceus* Fries [= *Strobilomyces floccopus* (Fries) Karst.] is caused by strobilomycol, a substance oxidized by laccase and yet at the same time phenol-like. The same appearance in *Russula nigricans* (Fries) Fries is caused by the oxidation of tyrosin under the influence of tyrosinase.

MISCELLANEOUS SUBSTANCES CONTAINED IN HYPHAE. In addition to the hyphae already discussed there are others of various form and size which contain resins, proteins, glycogen, dextrin and other substances. According to Heim (1936), *Marasmius oreades* (Fries) Fries has a cyaniferous network. Locquin (1944) reports

that cyanide-like substances appear in various parts of a considerable number of Hymenomycetes and are particularly abundant in the basidia. Zopf (1890, p. 355) found resin-containing substances in hyphae of *Pholiota spectabilis* (Fries) Gill. [= *Gymnopilus spectabilis* (Fries) Sing.] and related forms. Istvanffi and Johan-Olsen (1887) also found resin-secreting hyphae in several genera. Relatively thin resin tubes were observed in *Merulius* [in part = *Serpula*], while thicker tubes were seen in various species referred to *Hydnum*, *Polyporus* and *Trametes*. Lohwag (1938) found that in rhizomorphs of *Gyrophana lacrymans* (Fries) Pat. [= *Serpula lacrimans* (Fries) Schroet.] many parts of the vascular hyphae are stuffed full of proteins and resemble conducting organs in all characteristics, while adjoining parts of the same hyphae appear more or less empty. Lohwag felt that these could be considered as conducting organs in which nutritive materials had accumulated.

#### PSEUDOCYSTIDIA

Where the various kinds of vascular hyphae terminate at the sporocarp periphery, they frequently protrude slightly beyond the other peripheral elements and are conspicuous because of this and often also because of their contents, their greater diameter than adjoining elements, or other distinctive characteristics. Such forms appearing in the hymenium have sometimes been termed "cystidia" or "cystidioles", but their origin and usually their contents and nuclear condition show that they are distinct from true cystidia. They may be called "pseudocystidia".

Pseudocystidia occur in fungi which have vascular hyphae. Bambeke (1892b) found vascular hyphae in all of 100 species in 40 genera of agarics which he studied. In a great number of these the last ramifications of the hyphae were terminated by a free extremity protruding among the hymenial elements in the form of a "cystidium". Corda (1839, pl. 7, fig. 106), Boudier (1886), Massee (1887), Topin (1901, p. 73) Arnould and Goris (1907), Wager (1911) and Lohwag (1941, p. 389), among others, have called attention to the "cystidia" formed by the terminations of laticiferous hyphae in *Lactarius* and *Russula*. Maire (1910) found that the cystidium-like elements of *Russula* are sometimes, but not always, connected with the laticiferous vessels when these are pres-

ent in the gills. Heim (1943) was able to see that the "cystidia" of *Lactarius melanogalus* Heim, *L. adhaerens* Heim and *L. gymnocarpus* Heim are terminations of laticiferous tubes. A species of *Russula*, *R. fragilissima* Heim, was found to resemble *L. gymnocarpus* very closely in nearly all anatomical aspects, including the "cystidia", but the tubes in this *Russula* bear no latex. This led Heim to question the validity of the presence or absence of liquid latex as a criterion for separating the primitive *Lactario-Russulae* into separate genera. Istvanffi (1896a, 1896b) listed a number of species of *Stereum* which have tubiform conducting organs running at first parallel with the hymenial surface, then with their free extremities protruding into the hymenium and more or less swollen. These protruding apices are pseudocystidia, although Bourdot and Galzin (1928) and Pilát (1930) called them "cystidia". Burt (1920) ignored those of *S. fasciatum* (Schw.) Fries and related species, but called those of *S. ochraceo-flavum* (Schw.) Ellis "cystidia".

Since pseudocystidia often are referred to as "cystidia", it is evident that many of these hyphal tips protrude somewhat beyond the hymenial surface. Often this emergence is nearly imperceptible and probably is seldom over 15 micra or so. Smith and Hesler (1943), for example, have described the pleurocystidia (actually pleuropseudocystidia) of *Cortinarius subaustralis* A. H. Smith & Hesler as originating from the laticiferous hyphae of the trama and hardly protruding beyond the basidia. In such cases they may be recognized by their origin, form and contents. While most pseudocystidia appear to be the terminations of vascular hyphae, the ends of skeletal hyphae may protrude among the basidia in certain species, as in some Polyporaceae (Cunningham, 1946), and these likewise may be termed "pseudocystidia".

Since pseudocystidia usually are the apices of vascular hyphae, their contents are the same as those of the latter. Arnould and Goris (1907) used Ronceray's sulfovanillic reagent to stain the contents of hyphae and hymenial elements in several fungi. In some, such as *Tricholoma georgii* (Fries) Quél. [= *Calocybe gambosa* (Fries) Sing.] and *Collybia maculata* (Fries) Kummer, the various hymenial elements all were colored carmine by this reagent. In *Lactarius*, however, the basidia colored red, but the "cystidia" and laticiferous hyphae of most species were deep blue. The same



effect was obtained in several species of *Russula*, but not all. Kühner (1926) has found that the contents of the laticiferous hyphae of *Lactarius rufus* (Fries) Fries are similar to those of the "cystidia" and seem to consist of cytoplasm in the form of a dense but delicate reticulum. Topin (1901, p. 75) found that the contents of the "cystidia" and laticiferous vessels of *Lactarius* and *Russula* have similar contents and react similarly to treatment with various reagents. He reported that the contents of these "cystidia" are of a different nature in each of four rather distinct phases of basidiocarp development. When the basidiocarp is young, the "cystidial" contents are clear and homogeneous; in the second phase they are more granular and often somewhat yellow, or oily globules may appear; at the time of spore formation the oily globules become finely dispersed; at last the contents become vacuolar and mostly disappear, leaving a granular protoplasmic layer against the wall. It is in this final stage that incrusting matter appears on the exterior surface of the "cystidium". Wager (1911) reported large quantities of glycogen in the "cystidia" arising from the vascular hyphae of *L. rufus*. Bambeke (1895), studying *Lentinellus cochleatus* (Fries) Karst., found the vascular hyphae and their terminations difficult to see until they were treated with osmic acid. Bambeke thought that the black color obtained with this reagent revealed the presence of an essential oil forming the greater part of the contents of these hyphae. Kühner (1926) reported that some pseudocystidia of *Hygrocybe ovina* (Fries) Kühner have an apical cytoplasmic clot, while others appear completely empty.

Pseudocystidia are thought by many mycologists to serve as excretory elements. Massee (1887) and Wager (1911) reported excretion of glycogen from the apices of pseudocystidia. Bambeke (1895) concluded that the essential oil carried by the vascular hyphae of *Lentinellus cochleatus* is eliminated at their apices which thus serve as excretory elements and give off the anise-like odor of this fungus.

#### GLOEOCYSTIDIA

Gloeocystidia occur in many genera of Homobasidiomycetes as well as in some Tremellales of the Heterobasidiomycetes. Several genera have been characterized primarily by the fact that they possess gloeocystidia. Some of these are *Bourdotia* Bres., *Gloeo-*

*tulasnella* Höhn. & Litsch., *Seismosarca* Cke., *Gloeocystidium* Karst., *Gloeopeniophora* Höhn. & Litsch., *Dryodon* Quél. and *Parapterulicium* Corner (1952). In addition, Corner (1950, p. 19) has limited the clavarioid genera *Lachnocladium* and *Hormomitaria* to those species having gloeocystidia. Bresadola (1908), and later Burt (1915, 1926), Rogers (1933, 1935), McGuire (1941), and Martin (1944), treated *Bourdotia* as a subgenus of *Sebacina*. Bourdot and Galzin (1928, p. 247) felt that *Gloeopeniophora* was not a well-constituted genus because of the difficulty of making a clear distinction from *Peniophora*, and Rogers and Jackson (1943) have refused to recognize *Gloeocystidium* because they felt that it did not necessarily bring together related species. In addition to the genera which are characterized by the possession of gloeocystidia, there are numerous species in many other genera which have them. They seem to be especially prominent among the Polyporales, appearing in the genera *Trechispora*, *Stereum*, *Aleurodiscus* and *Merulius*, and, according to Cunningham (1946), in various species of Polyporaceae. Singer (1945) found that typical corticioid-type gloeocystidia occur in a number of species of *Favolaschia*.

Gloeocystidia are of varied form, some of them being nearly indistinguishable from submerged, non-incrusted cystidia, others being long, flexuous, refractile structures. Many of the short club-shaped and the globose elements which Istvanffi and Johan-Olsen (1887) and Istvanffi (1896) discussed as fat-containers now are known to be gloeocystidia. The typical gloeocystidium is an elongated, usually rather slender, tortuous object, sometimes slightly enlarged toward the base and with a long slender apical neck, sometimes slender over the entire length and then often tapering very gradually toward the apex. The walls are thin and colorless and there probably seldom or never are true septa. Höhnelt and Litschauer (1907) have reported that *Gloeocystidium oleosum* Höhn. & Litsch. [= *Peniophora pallidula* Bres. ex Bourd. & Galz.] has gloeocystidia with one to three septa which have clamp connections, but these structures are not gloeocystidia in any accepted sense. They are not readily classified but perhaps should be considered as thin-walled, septate, tramal cystidia. According to Bourdot and Galzin (1928, p. 247), the walls of gloeocystidia are never incrusted with crystalline particles. Often the apical neck of an elongated gloeo-

cystidium may collapse and is then unrecognizable; sometimes the entire gloeocystidium may collapse.

Whelden (1936) studied the development of cystidia and gloeocystidia in a fungus which he identified as *Peniophora livida* (Fries) Burt, although, according to Burt (1920), that species does not have gloeocystidia. Whelden's specimen obviously was misdetermined, and, unfortunately, no material was preserved for reference. Whelden found that at no time during their development is there any homology between cystidia and gloeocystidia in the species which he studied. In contrast to the cystidia, which Whelden observed originating from hyphal tips in no way distinguishable from basidium initials, gloeocystidia were found to originate as lateral branches of the mycelium, usually starting in the region near the substratum. Whelden concluded that these gloeocystidia represent unmodified hyphae which become much enlarged and stored with quantities of reserve materials. Bourdot and Galzin (1928, p. 247) said that gloeocystidia are organs of the same origin and the same nature as cystidia, but this very often is not the case. As shown by Whelden's study, and as Overholts (1929) has said, gloeocystidia are typically the enlarged terminations of otherwise unmodified hyphae. Certain cystidia also may originate as the apices of more or less unmodified hyphae, in which case they may be distinguished from gloeocystidia by their thicker or incrustated walls, their regular shape, their non-refractile contents, or perhaps by some other character which may indicate their true nature. Often, however, cystidia are seen to be borne and to originate in the basidial fascicles, which probably is very rarely true of gloeocystidia. Singer (1945) was able to show a very marked difference between pseudocystidia, as terminations of laticiferous hyphae in *Russula*, and gloeocystidia, which he studied in *Favolaschia*, by staining both elements with cresyl blue. Gloeocystidia exhibited a striking metachromatic reaction with this stain, the contents coloring bright blue and the walls lilac. Pseudocystidia of *Russula* did not show this metachromatic effect.

Although gloeocystidia are found in the hymenium and sometimes, although not frequently, even protrude beyond the hymenial surface, characteristically they are more deeply seated structures than most cystidia. Often they are seen to originate from near the substratum in species such as "*Peniophora livida*" of Whelden and



*Gloeocystidium inaequale* Höhn. & Litsch. [= *Corticium geogenium* Bres.]. Many other species have gloeocystidia originating in the region of the context or trama adjoining the subhymenium, or even in the subhymenium itself. Corner (1950) reported that the gloeocystidia of *Clavicornia* Doty (p. 285) are deep-seated structures which traverse the subhymenium and hymenium. He found that the gloeocystidia of *C. mairei* (Battetta) Corner (p. 291) and *C. tuba* (Heim) Doty (p. 294) originate from deep within the subhymenium or even from the trama. In *Lachnocladium* sensu Corner (p. 91) he found that the gloeocystidia are the earliest-formed hymenial elements and thus are deeply rooted in the subhymenium. The hymenial gloeocystidia of two species of *Parapterulicium* (Corner, 1952) were seen to originate from longitudinally oriented subhymenial hyphae.

Study of the nuclei in gloeocystidia is difficult because of the dense and refractile cell contents. In *Sebacina* subg. *Bourdotia*, Whelden (1935) found that the two nuclei of the gloeocystidium may disintegrate at a very early stage. On the other hand, they may pair near the center of the young gloeocystidium and often may migrate into the elongating apical tube as the gloeocystidium continues its development. There they eventually disintegrate either before or after fusion. Kühner (1926) reported disintegration of nuclei in gloeocystidia of *Sebacina gloeocystidiata* Kühner [= *Sebacina* (*Bourdotia*) *cinerea* Bres.]. Wittlake (1938) found two nuclei in younger stages of gloeocystidia in a fungus which he referred to as *Sebacina calcea* (Pers.) Bres. The nuclei later migrated toward the denser cytoplasm at the distal end of the gloeocystidium, and eventually both the cytoplasm and nuclei disappeared. According to Martin (1944), *S. calcea* does not have gloeocystidia. Whelden (1936) determined that the nuclei in gloeocystidia of "*Peniophora livida*" probably are few and variable in number, and that they eventually disintegrate.

The contents of gloeocystidia are either colorless or yellowish, granular and refractile, or homogeneous and glassy-appearing, usually very dense and not exuding in the form of a latex when the gloeocystidium is broken. Whelden (1935) has described the contents of gloeocystidia of *Sebacina* (*Bourdotia*) *deminuta* Bourd. in considerable detail. The protoplasm of the gloeocystidium becomes progressively thinner as the latter develops, and increasing quanti-

ties of oil-like droplets accumulate. In the apical tube there is developed a uniformly distributed but very thin protoplasm and many oil-like droplets. Most of the protoplasm disappears and the tube collapses after nuclear disintegration. Final development of the gloeocystidium leads to the exhaustion of the oily-appearing contents, leaving an empty, partially collapsed object which resembles a small cystidium. In "*Peniophora livida*", Whelden (1936) found that the gloeocystidium at first has densely staining contents in which are seen many spherical droplets of variable size and distribution. Later the contents become increasingly thinner and eventually remain only as a few scattered droplets of densely staining substance located along the wall. Bourdot and Galzin (1928, p. 247) described the contents of gloeocystidia as often being a hyaline liquid of a composition approximating the sap of a basidium. It must be remembered, however, that Bourdot and Galzin considered gloeocystidia as not differing from young, thin-walled, submerged cystidia, and this description of the contents seems to fit such structures very well. At other times Bourdot and Galzin found the contents to be full of droplets which are more or less yellowish, or to contain glycogenous materials which turn brown in contact with iodine solution. They described the contents of gloeocystidia in *Stereum murrayi* (Berk. & Curt.) Burt as being granular, hyaline or amber, finally resinoid masses.

According to Lohwag (1941, p. 398), the gloeocystidia with oily-resinous contents belong in the sap-hyphal system with excretory function. He believes they also are storage reservoirs. The latter idea was expressed also by Overholts (1929) and by Whelden (1936), the latter describing the contents of gloeocystidia of "*Peniophora livida*" as becoming increasingly thinner, apparently being drawn upon to supply nutrient substance for the developing basidiocarp. He said that all indications point to a condition exactly like that of any unmodified hypha, one which merely has become enlarged and stored with quantities of reserve substance.

**PILEOGLOEOCYSTIDIA.** Lohwag (1941, p. 402) has called attention to the fact that gloeocystidia may appear in various parts of the pileate fungi, not being restricted necessarily to the lamellae. The more or less broadened ends of oil hyphae occur very abundantly in the loose trichoderm of the cap of *Flammula dilepis* Berk. & Br. [= *Gymnopilus dilepis* (Berk. & Br.) Sacc.]. Lohwag sug-

gested that these could be designated as "dermatogloeocystidia" or "pileogloeocystidia".

**VESICULAR BODIES.** Closely related to gloeocystidia in their method of origin and often also by their contents are a number of structures descriptively termed "vesicular bodies". These elements occur in the context and subhymenium of various Hymenomycetes. Often, as in some species of *Corticium*, they appear as gloeocystidia which eventually lose their contents and remain as empty sacs. *Stereum purpureum* (Fries) Fries has subglobose vesicles which may be empty or may contain a yellowish refractile material. The origin of these vesicles as terminal enlargements of otherwise unmodified hyphae may be observed when the fungus is cultured on agar. The context of *S. murraii* (Berk. & Curt.) Burt is made up almost entirely of vesicular bodies. The gloeocystidia which appear in the hymenium of this species are said, by Rogers and Jackson (1943), to be elongated vesicular bodies. These elements thus do not seem to be fundamentally different from gloeocystidia, but are distinguished on the basis of their more regularly subglobose to ovoid shape and by the fact that so frequently they appear to lack contents or to have inconspicuous contents.

#### SETAE

Setae differ from most cystidia by their brown color and by the fact that they are borne only in xanthochroic basidiocarps, although cystidia also may be found in some brown-context sporocarps. I have found that the seta-like cystidia of *Stereum abietinum* (Fries) Fries and *S. chailletii* (Fries) Fries have a clamp connection at their base, while true setae lacked clamp connections in several species of *Hymenochaete* and *Fomes* which I examined. According to Corner (1950, p. 22), xanthochroic basidiocarps always lack clamp connections. It is not at all unusual to see setae referred to as "colored cystidia" or, on the other hand, to find elongated cystidia referred to as "setae". Since these terms have come to have a very particular meaning, they should not be applied loosely. The genus *Hymenochaete* of the Thelephoraceae is characterized by having setae. Many species of the xanthochroic Polyporaceae bear these structures. In the clavarioid fungi Corner (1950, pp. 42, 268) has described the genus *Clavariachaete* as bearing hymenial setae of the type found in *Hymenochaete*.



The characteristic "conducting organs" of Group I in Istvanffi's (1896a, 1896b) system are setae. These organs were characterized by Istvanffi as being tubiform and undulate with the pointed extremity protruding beyond the hymenial surface. Setae usually are rather slender, elongate, tapering, subulate or sometimes ventricose, simple or sometimes substellate, brown, non-septate spines with thick walls that become darker brown when moistened with potassium hydroxide solution. Burt (1920) has stressed this reaction in distinguishing brown cystidia found in a few species of *Stereum* from the setae of *Hymenochaete*. Setae usually are not incrustated and at the most have a glassy jacket over the apical region that should not be mistaken for the incrusting matter of cystidia. Setae often protrude considerably beyond the hymenial surface. At their basal end they gradually taper to the diameter of the context hyphae. Setae of rather unusual form are found in *Polyporus circinatus* Fries [= *P. tomentosus* Fries var. *circinatus* (Fries) Haddow]. As illustrated by Haddow (1941) and by Coker (1946), these have distinctive hook-like recurved apices.

Setae may occur in various parts of the basidiocarp. Those that are in other parts of the fruiting body than the hymenium may be designated, for example, by terms such as "pileosetae" or "embedded setae". The hymenial setae usually are oriented perpendicular to the hymenial surface, so that they are parallel with the basidia. They do not always protrude, some remaining buried in the hymenium or subhymenium. The position of setae and related bodies in the basidiocarp may have a decided influence upon their form. Corner (1948b) has studied this subject as it is revealed in the sporocarp of *Asterodon*, a genus in the Hydnaceae characterized by stellate setae throughout the interior of the fructification. Stellate setae are compound setae whose multidirectional outgrowth, according to Corner, represents the uninhibited growth of hyphae within the loose hyphal web of the resupinate context. In the subhymenium, orientation of growth becomes more unidirectional, so that lateral branching of the setae is suppressed, the ultimate of this unidirectional influence appearing in the unbranched setae of the spines where the peripheral extrahymenial setae come within the influence of the hymenial factor near the tip of the spine. Embedded setae may be unbranched because they are oriented in the plane of a strong unidirectional growth influence as, for example,

the embedded setae in the spines of *Asterodon* and in the trama of the dissepiments in various Polyporaceae.

Lohwag (1937) classified setae as belonging among the tramal cystidia because they originate in the trama. Masee (1889) found that the setae of *Hymenochaete* originate from colorless, thin-walled, septate hyphae of the "subiculum" [context]. Corner (1950, p. 268) described the setae of *Clavariachaete* as arising deeply in the thick subhymenium. Brown (1915) wrote that the setae of *Hymenochaete rubiginosa* (Fries) Lév. gradually taper below into thin-walled hyphae which extend horizontally. Lohwag (1929) found that the thick-walled condition and brown color of the setae in *Xanthochrous cuticularis* (Fries) Pat. [= *Polyporus cuticularis* Fries] extend throughout the length of the seta and its stalk mostly to the first cross-wall, so that the adjoining hyphal cells are distinguishable in no respect from those of the other tramal hyphae. Lohwag says that Pilát's (1942, p. 565) illustration of these structures would lead one to believe that the setae arise from long thick-walled tubes without cross-walls but that the latter really represent rather long setae extending from the trama. Hymenial setae of this species are illustrated also by Joachim (1931).

Corner and Cunningham have discussed setae in relation to the various systems of hyphae in the basidiocarp. Corner has studied the kinds of hyphae in various hymenophores in the Polyporaceae and has identified such series of hyphae as generative, skeletal and binding. Originally (1932a) he described a mediate series, but this now (Cunningham, 1946) is regarded as merely a part of the skeletal series. In a fungus with only one series of hyphae, this must always be generative and the hyphal system is called monomitic. Dimitic systems have generative and skeletal series, while trimitic systems have all three series. Corner (1932b) found that *Fomes levigatus* Corner has generative hyphae which are branched, septate, and lack clamp connections, while the skeletal hyphae are unbranched, aseptate, and have thick, dark, yellow-brown walls. The setae in this species were found to originate from the ends of thick-walled generative hyphae where the latter reach the surface. In other words, although the skeletal hyphae are thick-walled, non-septate and colored like the setae, the latter do not arise from them. On the other hand, Cunningham (1946) reported that the setae of

species having monomitic systems arise from the generative hyphae but that in dimitic species of brown *Poria* and other Polyporaceae with brown hyphae they arise from skeletal hyphae. I found that the setae arise from septate hyphae in *Fomes pini* (Fries) Karst., *Hymenochaete badio-ferruginea* (Mont.) Lév., *H. cinnamomea* (Fries) Bres., *H. curtisii* (Berk.) Morg., *H. rubiginosa* (Fries) Lév., *H. sallei* Berk. & Curt. and *H. tabacina* (Fries) Lév. Setae have not been recorded in species known to have a trimitic system. *Asterodon ferruginosum* Pat. is dimitic according to Corner (1948b). The thick-walled, aseptate, brownish skeletal hyphae end obliquely in the hymenium or subhymenium or against the substratum, and have simple cylindrical tips. Setae of this species were observed to arise from the generative hyphae and to be entirely distinct from the skeletal hyphae.

Istvanffi (1896a, 1896b) considered setae to be nothing more than the terminations of tubiform conducting elements. This appears to be untrue in the light of Corner's and my observations. Overholts (1929) was undecided about their activities, but he suggested that when in the context or trama they might give rigidity to that region. He, and also Buller (1909, p. 18), suggested that they may serve as protection against slugs or other animal parasites. Lohwag (1926, 1937) has maintained that setae may be considered homologous with the capillitium of the Gasteromycetes.

Elements which have been termed "false setae" (Talbot, 1951) occur in *Duportella* and a few other Hymenomycetes. These originate as skeletal hyphae which assume a vertical position and have a deep yellow-brown color which becomes darker in potassium hydroxide solution. They are moderately thin-walled as compared to true setae, and in *D. tristicula* (Berk. & Br.) Reinking they are immersed in later stages of basidiocarp development.

**EMBEDDED SETAE.** Embedded setae are found in the context or trama of many species of xanthochroic Polyporaceae, including *Polyporus glomeratus* Peck (Overholts, 1917), *P. tabacinus* Mont. (Cunningham, 1946), *Fomes pachyphloeus* (Pat.) Bres. (Lloyd, 1915; Humphrey and Leus, 1932), *F. lamaoensis* (Murr.) Sacc. & Trott. (Overholts, 1929), *Xanthochrous patouillardii* (Rick) Heim var. *congoensis* Pat. & Heim [= *Polyporus patouillardii* (Rick) Theiss. var. *congoensis* (Pat. & Heim) Hendrickx] (Heim, 1933), *Poria contigua* (Fries) Karst. and *P. obliqua* (Fries) Karst.



(Lohwag, 1936) and *P. weirii* Murr. (Nobles, 1948). They also occur in *Asterodon ferruginosum* (Corner, 1948b) and various other species with xanthochroic basidiocarps.

Embedded setae usually have the form of elongated, brown, thick-walled sharp to rather blunt tubes that extend in a direction parallel with the tramal hyphae. They are likely to vary considerably in length and may be larger than the ordinary hymenial setae. Overholts (1917) found that the embedded seta of *Polyporus glomeratus* is of largest diameter just back of the pointed apex and that it gradually tapers toward its base. In *Asterodon* (Corner, 1948b) stellate setae appear in the context of the resupinate part of the basidiocarp; in the trama of the spines, though, there are simple or once-bifurcate embedded setae which extend in a direction parallel with the long axis of the spine.

Embedded setae may be distributed throughout the sporocarp or may be confined mostly to the context or to the trama of the dissepiments or spines. Lohwag (1936) found that the embedded setae of *Poria contigua* originate from hyphae arising from the substratum but are overgrown as the sporocarp grows and then are found in the context of the basidiocarp and at the base of the dissepiments. In *Fomes pachyphloeus* and *Polyporus glomeratus* it was noted that the embedded setae arise as modifications of the ends of ordinary context or tramal hyphae; the transition may be gradual or abrupt. Corner (1948b) saw that the extrahymenial setae in the spines of a dimitic species of *Asterodon* are borne on stalks which have arisen from the generative hyphae. As a general rule, it appears that embedded setae arise from septate hyphae of the context or trama and are distinguished from these hyphae by being non-septate, thicker-walled and of much darker color. In all these attributes they resemble the hymenial setae.

**STELLATE SETAE.** Stellate setae are very much like ordinary hymenial setae in their color, absence of incrustation, and in their relation to the ordinary hyphae of the sporocarp. They differ from simple setae by being complex bodies which have several radiating spines. There are instances of transition in form to simple setae and to the dichotomously-branched elements of *Vararia*. Stellate setae occur in a few genera of Thelephoraceae and Hydnaceae, particularly in *Asterostroma* and *Asterodon*, although those of *Asterostroma* show characteristics intermediate between the dichophyses

of *Vararia* and the typical stellate setae of *Asterodon*. Substellate setae transitional to simple setae occur in *Asterostroma degenerans* Bres., and forms transitional to dichophyses in *A. muscicola* (Berk. & Curt.) Mass. *Lachnocladium brasiliense* Lév. (Burt, 1919) has both antler-shaped bodies suggestive of dichophyses and stellate bodies suggestive of the stellate setae of *Asterodon*. *Stelligera membranacea* Heim (1938, 1949) of the Clavariaceae also has forms varying from fairly typical stellate setae having four to eight radiating arms to dichophyses which are scarcely different from those of *Vararia*. The stellate setae of this species are the most conspicuous elements in the context and cause it to have a brownish color. The typical stellate seta has a number of radiating arms which are situated mostly in a plane parallel with the hymenial surface. Masee (1889, p. 117) mentions three to seven rays in the stellate setae of *Asterostroma*, while Corner (1948b) found that the stellate setae in the resupinate context of *Asterodon ferruginosum* have four to six acute arms.

Ainsworth and Bisby (1950, p. 29) have defined an "asterophysis" as a stalked, stellate, sterile structure, as in the hymenium of *Asterostroma*. The sporocarp of *Asterodon* is of the xanthochroic nature, as found in *Hymenochaete* and many Polyporaceae. The sporocarp of *Asterostroma* is not xanthochroic. While the stellate setae of *Asterostroma* show relations with the dichophyses of *Vararia*, it is convenient at present to classify them with the stellate setae of *Asterodon* and to reject the term "asterophysis" for any of these elements. In case the distant position of *Asterostroma* from *Asterodon* and the transitional nature of the stellate bodies in *Asterostroma* indicate a distinctive name for these bodies, it still seems preferable to eliminate the term "asterophysis" altogether. Corner's (1948b) discussion of the changes of form of stellate setae to conform with the form factors of the sporocarp already has been mentioned. Stellate setae, according to Corner's concept, differ from simple embedded setae because they are not subjected to growth-form influences which would cause their growth to be projected in a single direction. In other words, the stellate structure represents the uninhibited form of growth, while the embedded setae are subjected to a strong unidirectional influence, as in the descending hyphal growth of a polyporaceous dissepiment or a hydneous spine. Corner found that the largest stellate setae

of *Asterostroma* occur in the basal region of the context and that they decrease in size toward the hymenium.

According to Corner, the basidiocarp of *Asterostroma* is monomitic, which means that only generative hyphae are present. Some of these septate, hyaline, thin-walled, branching hyphae give rise to the brown, stellate setae of the context, while others eventually give rise to the basidia which form the hymenium. In *Asterodon ferruginosum* the stalk of the stellate seta originates from the generative hypha, which is septate, lacks clamp connections and has thin and colorless or only slightly thickened walls. Both stellate setae and skeletal hyphae arise as modified laterals of the generative hyphae in this fungus, but always independently. The stellate setae of *Stelligera membranacea* Heim (1938, 1949) are borne on thin- or thick-walled, septate hyphae which Heim calls "connective hyphae". In his opinion, the presence of stellate setae in representatives of several families is of interest as an indication of relationships not accounted for by the traditional Friesian system.

**PILEOSETAE.** Seta-like bodies may protrude from the superior surface of sporocarps of various species, particularly among the Polyporaceae. Buller (1924, p. 53) used the term "pilocystidia" (pileocystidia) to designate similarly situated cystidiform structures; therefore setae borne on the superior surface of the pileus may be called "pileosetae". These may be simple, brown, pointed hairs, or they may have a few short, spiny branches. They have been found on the caps of *Fomes pachyphloeus*, *Polyporus cuticularis* and other species of the Polyporaceae. Josserand and Kühner (1933) described slender, acicular, brown pileus hairs in *Marasmius torquescens* Quél. which bear a considerable resemblance to pileosetae, but the authors do not indicate whether they darken in potassium hydroxide solution.

Humphrey and Leus (1932) found that the seta-like structures occur throughout the sporocarp of *Fomes pachyphloeus*. Some of these protrude through the young crust as yellowish-brown to dark reddish-brown, thick-walled setae. Patouillard (1923, 1924) likewise reported that erect cystidiform bristles, analogous to those in the trama, grow on the upper surface of sporocarps in this species. Lohwag (1929) described the pileosetae of *Polyporus cuticularis* as being brown, thick-walled, longer than hymenial setae, and possessing two to several variously-formed spiny prolongations which

often are in one or more whorls near the apex of the seta. Joachim (1931) has illustrated two such pileosetae.

According to Humphrey and Leus, the pileosetae of *Fomes pachyphloeus* originate as modifications of the ends of ordinary tramal hyphae. In some cases there is an abrupt change from hypha to seta, but usually there is a very gradual transition in color, size and shape. They follow the course of the ordinary hyphae and then protrude through the young crust. Lohwag (1929, 1930) has illustrated the origin of the pileosetae in *Polyporus cuticularis*. An ordinary yellowish tramal hypha of the cap bears a short side-branch from which the seta originates. By its dark brown color the seta contrasts sharply with the cell that bears it. Lohwag says that it is not strange to find setae growing from the superior surface of the cap; he believes that this is an expression of the ancestral condition of fertility of the cap surface and the basic homology of all binucleate cells of the basidiocarp.

#### DICHOPHYSES

Höhnelt and Litschauer (1907) set up the genus *Asterostromella* [= *Vararia* Karst.] to include species having regularly dichotomously-branched elements which Pilát (1926) termed "dichophyses". Some of the species which have typical dichophyses or structures closely approximating them are *V. investiens* (Schw.) Karst., *V. pallescens* (Schw.) Rogers & Jacks. [the former *Asterostromella dura* Bourd. & Galz. or *Dichostereum durum* (Bourd. & Galz.) Pilát] and *V. phyllophila* (Mass.) Rogers & Jacks [the same as *Asterostromella epiphylla* (Pers. ex Fries ?) Höhn. & Litsch., which is the type species of *Asterostromella*]. In addition, Corner (1948b) says that some tropical species of *Hymenochaete* have dichophyses. *Lachnocladium brasiliense* Lév. has elements varying in structure from substellate to regularly dichotomous. Corner (1952) has described hymenial dichophyses in *Parapterulicium subarbusculum* Corner. These arise from the subhymenial generative hyphae and are three to six times dichotomous, ending in straight or flexuous filiform tips. Singer found structures which he termed "dichophyses" in the superior surface layer of *Asterotus dealbatus* (Berk.) Sing. (1943) and in the cuticular layer of *Campanella* (1945). He says that these structures are comparable to the dichophyses of *Vararia*.



Dichophyses are elements having a limited growth which takes the form of rigid regularly dichotomous branching with internodes tapering until they end in acute colorless tips. The dichophyses of *Lachnocladium* are described by Corner (1950) as being aseptate with thickened, pale yellow or brownish-yellow walls, but colorless at the acute tips. According to Corner (1948*b*), stellate setae appear to be regularized dichophyses with simple arms.

Dichophyses constitute nearly the entire context of many species in which they occur and also may be found in the hymenium. Corner (1948*b*) says that they originate as lateral branches of the generative hyphae but that the latter are exceedingly tenuous and thus not seen very easily. He (1950) wrote that the dichophyses of *Lachnocladium* arise either on lateral hyphae of limited growth or terminally.

#### TRAMAL CYSTIDIA

In addition to pseudocystidia, a number of other cystidiform elements may originate in the context or trama. Some of these are setae, gloecystidia and the true cystidia of tramal origin or, more succinctly, the tramal cystidia. Darker forms of tramal cystidia may be mistaken for setae, but usually there are characters such as shape, incrustation or method of origin which are helpful in distinguishing them. The distinction between tramal cystidia and gloecystidia may be difficult to make at times, and Lohwag (1941, p. 39) classes gloecystidia as a particular type of tramal cystidium characterized by oily resinous contents. In theory, hymenial cystidia arise along with the basidia in the basidial fascicles, while tramal cystidia have a deeper origin. Actually this may be very difficult to ascertain. Generally it may be said that any cystidia that originate at approximately the same general level as the basidia may be classed as hymenial cystidia. Their origin and nature are analogous to, and perhaps homologous with, those of the basidia. Cystidia which arise from a deeper stratum, generally in the context or trama, may be considered tramal cystidia. Their position in the basidiocarp would seem to make any analogy between tramal cystidia and basidia difficult to defend.

Tramal cystidia are found in many species of Basidiomycetes, for example, in *Physalacria inflata* (Fries) Peck (McGuire, 1939), in various species of *Stereum*, *Peniophora*, *Tomentellina* (Bourdot and Galzin, 1928), *Cantharellus* (Boudier, 1886), *Polyporus* and

*Fomes* (Ames, 1913), in *Trametes pini* (Fries) Fries [= *Fomes pini* (Fries) Karst.], *Odontia* (Miller, 1934), *Collybia apalosarca* Berk. & Br. (Corner, 1934), *Hygrophorus firmus* Berk. & Br. var. *straliotes* Corner and *H. hypohaemactus* Corner (Corner, 1936), *Panaeolus fimicola* (Fries) Gill. (Godfrin, 1902) and *Inocybe* (Heim, 1931, p. 39). A number of these structures in *Peniophora* are illustrated by Bourdot and Galzin (1928). Their drawings show that, while some cystidia easily are determined to be of tramal origin, there are transitional forms of which some originate in the subhymenium and some at deeper levels.

As Lohwag (1941, p. 39) has written, tramal cystidia represent terminations of tramal hyphae and may, therefore, be septate and have clamp connections, although this is by no means the rule. Cystidia of *Peniophora byssoides* (Fries) Bres. ap. Brinkm. often are one- to four-septate with clamp connections, and *P. subtestacea* Litsch. also possesses septate tramal cystidia with thickenings at the septa which evidently represent vestiges of clamp connections. Some thick-walled, non-incrusted tramal cystidia of *Peniophora* have a rather close similarity to pseudocystidia, but usually they are recognizable as true cystidia. In the Polyporaceae, according to Ames (1913), some cystidia are merely the inflated rounded ends of hyphae. This also is the case in some species of *Odontia*. In *O. stipata* (Fries) Quél. (Bourdot and Galzin, 1928, p. 419) the cystidia are nothing more than axillary hyphae which are distinguished by their thickened walls. The cystidia of *Stereum umbrinum* Berk. & Curt. originate from deep within the context, although there is little differentiation until they approach the hymenium. According to Talbot (1951), these cystidia are terminations of skeletal hyphae which are reminiscent of the false setae of *Duportella*, but they do not darken in potassium hydroxide solution. In *Physalacria inflata* (McGuire, 1939) the cystidia originate from deep within the context of the head and appear as thick clavate structures somewhat constricted back of the broadly rounded tip; they are heavily incrusted.

In their origin tramal cystidia often differ from pseudocystidia by arising from septate hyphae. Thus the pleurocystidia of *Collybia apalosarca*, as described by Corner (1934), appear to represent hyphal ends which have failed to delimit subhymenial cells but which elongate directly into cystidia, passing from the trama through the subhymenium by means of a long stalk. Corner

(1936) also has shown a similar occurrence in *Hygrophorus hypohaemactus*. Some of the laterals of the tramal hyphae fail to engage in the production of basidial fascicles but pass from the trama to the subhymenium as embedded, elongate, fusiform cells, or may pass beyond the hymenial surface and protrude up to fifty micra. Godfrin (1902) has shown that the cystidia of *Panaeolus fimicola* originate in a similar way, arising from the hyphae of the trama and passing directly through the subhymenium and into the hymenium. In various species of *Peniophora*, cystidia may be seen to originate from various parts of the context, even from the basal layer adjoining the substratum. They may remain submerged or may protrude beyond the hymenial surface.

The contents of tramal cystidia seem to be similar to those of hymenial cystidia and usually different from those of pseudocystidia and gloeocystidia. In *Collybia apalosarca* (Corner, 1934) the pleurocystidia have clear vacuolate contents. The tramal "cystidi-form hairs" of *Mycena* (Heim, 1931, p. 40) have a generally clear and homogeneous protoplasm. The tramal cystidia of *Hygrophorus hypohaemactus*, however, are said by Corner (1934) to have densely granular oleaginous contents. McGuire (1939) found that the tramal cystidia of *Physalacria inflata* usually take a deep stain with iron-alum-haematoxylin.

Tramal cystidia may develop very early and, as Lohwag (1941, pp. 163-164) has indicated, may serve as props by means of which the loose hyphal network rises from the substratum. The cystidia of *Peniophora chaetophora* Höhn. & Litsch. afford an example of this. The surface incrustation and the very thin apex of some tramal cystidia have suggested to various authors (Masse, Knoll, Lohwag) that these structures may serve as hydathodes. Knoll (1912) has cited the mucilaginous covering and abundant crystalline matter over the thin-walled apices of cystidia in *Peniophora glebulosa* (Fries) Sacc. & Syd. and other species as justifying this conclusion. Since this phenomenon occurs in connection with both tramal and hymenial cystidia, it will be discussed in more detail in the following section.

#### HYMENIAL CYSTIDIA

Hymenial cystidia are true cystidia which originate at about the same level as the basidia. Sometimes they can be seen to originate in the basidial fascicle. They are distinct from tramal cystidia and

from the protruding tips of vascular hyphae which form pseudo-cystidia. Hymenial cystidia occur in practically all cystidium-bearing groups of Basidiomycetes. In the Thelephoraceae they may be found in a number of genera, including *Pellicularia*, *Coniophora*, *Tomentella*, *Podostrombium*, *Peniophora* and *Stereum*. Cooke (1879) devised the term "metuloid" which he applied to the incrustated cystidia of *Peniophora*. In the clavarioid fungi, Corner (1950) has reported that relatively few species have true cystidia, most of the so-called "cystidia" actually being cystidioles. However, very conspicuous thick-walled cystidia are found in *Clavulina leveilleyi* (Sacc.) Overeem, in some species of *Physalacria* and in all species of *Chaetotyphula* and *Dimorphocystis*. In the Hydnaceae, cystidia may be observed in *Odontia* and *Steccherinum*. In the Polyporaceae they occur in *Polyporus*, *Fomes*, *Poria*, *Favolus* and *Boletus*. They are to be seen in many genera of the Agaricaceae, a few of which are *Clitocybe*, *Collybia*, *Lepiota*, *Mycena*, *Omphalia*, *Pleurotus*, *Russula*, *Pluteus*, *Hebeloma*, *Inocybe*, *Pholiota*, *Agaricus*, *Coprinus*, *Gomphidius*, *Panaeolus*, *Psathyra*, *Psathyrella*, *Psiilocybe* and *Stropharia*. Cystidia exist also in a number of genera in the Heterobasidiomycetes and Gasteromycetes.

The forms of hymenial cystidia are exceedingly diverse, varying from simple, hyaline, cylindrical, hair-like structures to forms heavily incrustated with crystalline matter over the entire surface or at the tip, or sometimes in rings or limited areas of the wall. At times the cystidia may bear branching or sterigma-like protrusions. Corner (1950, p. 400), for example, has described the genus *Dimorphocystis* as having both ordinary conical cystidia and cystidia with an irregularly lobed apex. In addition, he found forms transitional between the two. Intermediate forms greatly complicate the classification of cystidiiform elements. Cystidia, cystidioles, acanthophyses and dendrophyses show so many interrelations that only a thorough study of their origin, position and form ultimately can produce order in the classification of these elements.

Cystidia often are described as originating at the deepest level of the subhymenium or the outer part of the trama. In these cases it may be difficult to decide by reading the literature, or even by examining specimens, whether they are tramal cystidia or hymenial cystidia. *Pluteus cervinus* (Sacc.) Kummer is an example of this. According to Buller (1924, p. 105), the cystidia of this species



arise from the outer cells of the trama just beneath the subhymenium. The same is true of various species in *Peniophora* and other genera. In *Dimorphocystis*, Corner (1950, p. 400) found that the conical cystidia arise from the medullary hyphae or from the basal subhymenial hyphae as the primary hymenial elements, while the lobed cystidia of the same species were found to be of much more superficial origin. In *Chaetothyphula hyalina* (Jung.) Corner (1950, p. 211), the cystidia were seen to originate deeply in the subhymenium.

The forms taken by some cystidia, together with their place of origin and certain nuclear phenomena, have caused many mycologists to consider them as sterile basidia. Corner (1947) analyzed the forms of cystidia in *Clavaria* and *Oudemansiella* and concluded that very evident homologies with the basidia of those groups permitted the cystidia to be utilized for mathematical calculations that ordinarily would be carried out with basidia, the main difference in the form of these structures being that the apices of the cystidia become attenuated and fail to produce sterigmata. According to Buller (1922, p. 3), cystidia of Agaricaceae are sterile elements differing from "paraphyses" in their larger size, peculiar form, smaller number and often in the nature of their walls and contents. The cystidia of *Stereum purpureum* (Fries) Fries represent the very simple form with a transparent, non-incrusted membrane and hyaline, homogeneous protoplasm. The cystidium of this species is filiform-cylindrical and of the same diameter as the basidium, but occasionally somewhat swollen at the hymenial surface. This kind of structure properly is called a "cystidiole". Very simple forms are found also in various agarics. In *Inocybe* (Kauffman, 1921; Heim, 1931; Heim and Romagnesi, 1931) they are sac-shaped or rounded-clavate, shorter than most cystidia, and with a thin non-refractile wall which lacks incrustation. In addition to these inconspicuous cells, there may be larger elements which often are thick-walled, refractile, and which bear an apical crystalline mass. Similar cystidiform cells and well-differentiated cystidia are found in other genera as well. In general it is better to refer to the thin-walled, non-refractile, slender, often little-protruding cells as "cystidioles", while reserving the term "cystidium" for the more conspicuous and more strongly differentiated elements. In some instances, though, the simple, non-incrusted, cylindrical forms are

so greatly enlarged that they are considered cystidia, rather than cystidioles. An example is the kind in *Coprinus atramentarius* (Fries) Fries. According to Buller (1910; 1924, pp. 274-275), the cystidia of this species are some of the largest cells in the fungi, reaching a length of 170 or occasionally 210 micra and a width as great as 30 micra. Topin (1901, p. 43) examined these large cystidia in a number of species of *Coprinus* and found that they never were incrustated. Romagnesi (1944) used the term "leptocystidium" in reference to large thin-walled cystidia, and "lamprocystidium" for the type having thick refractile walls.

Several interesting modifications of cystidial form should be mentioned. First is the fact that some species may have septate cystidia. Rogers (1943), for example, has described septate cystidia in *Pellicularia langloisii* (Pat.) Rogers and *P. cystidiata* Rogers. Another modification, one which has caused much speculation concerning the nature of cystidia, is the formation of finger-like or sterigma-like outgrowths from the cystidial surface in several species. These may be scattered at random over the exposed surface of the cystidium or may be limited more or less to the apex. Fayod (1889) examined outgrowths of this type on cystidia of *Pluteus* and concluded that they represent hypertrophied sterigmata, the cystidia thus being modified basidia. Cystidia, cystidioles and basidioles all may show such protuberances. Depending upon the abundance and form of these outgrowths, the elements which bear them may be called "acanthophyses" or "dendrophyses". The aculeate basidioles in several species of *Stereum* are very similar in form to the horned cystidia of *Pluteus*. Somewhat more elaborately modified are the bottle-brush cystidia which Kühner (1938) and Smith (1947) have described in *Mycena*. Smith's illustrations of the various forms show almost every conceivable variation of contour and of surface-processes. Singer (1926) has described appendiculate cystidia which he detected in some species of *Russula*. These have apical prolongations which may range in length from one to 22 micra.

In the agarics there is occasionally a dimorphism of the cystidia on the gill sides (pleurocystidia) as contrasted with those on the gill edge (cheilocystidia) of a particular species. Kühner (1938, pp. 232, 400 and figs. 74, 129, 130) mentions such a dimorphism in *Mycena erubescens* Höhn., *M. rosella* (Fries) Kummer sensu Schröet., and *M. tenax* A. H. Smith, in which the facial cystidia

are fusiform and smooth, while the marginal cystidia are of bottle-brush form. Josserand (1936) discussed such dimorphism of cystidia in *Pluteus cervinus* (Secr.) Kummer. He found facial cystidia with apical hooks, while the edges of the long lamellae had cystidia lacking the hooks. On the short lamellae the situation was the same as that of the long lamellae on the two faces and on the part of the lamellar edge parallel with the edges of the long lamellae. But the short lamellae had, in addition, a posterior receding margin which had cystidia with the same kind of hooked apices as were found on the lamellar faces. Josserand explained this by the fact that the cystidia of the horizontal edges of the long and short lamellae were in contact with the stipe during their development and thus did not develop as fully as the others. But he mentioned that Kühner had suggested another, and decidedly novel, explanation for this dimorphism. According to Kühner's interpretation, there is one type of cystidium on the faces and another type on the horizontal edges of both long and short lamellae. The long lamella has only a horizontal edge, but the short lamella has also a posterior receding edge. The short lamella thus may be said to have three concrete dimensions: (a) a long lateral dimension extending from its posterior receding edge to its connection with the margin of the pileus; (b) a short lateral dimension extending from one face directly through the trama to the opposite face; (c) a vertical dimension extending from the juncture of the lamella with the context of the pileus down to the edge of the lamella. If the long lateral dimension becomes greatly reduced so that it equals the short lateral dimension, and both of these are considerably exceeded by the vertical dimension, then the shape of the lamella is so altered that it resembles that of a spine of *Hydnum*, and the posterior receding edge, along with the lamellar faces, has become the side of the spine. The horizontal edge is then the tip of the spine. The analogy of the posterior receding edge to the two faces when the lamella is thus compressed would explain why both should be expected to have the same kind of cystidia, while the cystidia of the horizontal edge of the lamella, which has become the tip of the spine, might be a different kind. *P. cervinus* is not the only species with cystidia having apical horns. According to Smith (1949, p. 444), they are found also in *P. umbrosus* (Fries) Kummer sensu Ricken and *P. salicinus* (Fries) Kummer.

Snell (1945) has described an unusual cystidial phenomenon

which he observed in the hymenium of certain *Boleti*. Yellow-brown bodies, varying considerably in size and shape, appear in the hymenium of a number of species. Snell noted that a regular series can be demonstrated from hyaline cystidia to cystidia with progressively darkening contents, closing off of the ventral part, and disappearance of the old cystidial wall which has enveloped the developing brown body. Finally the cystidium completely disappears and only the brown body remains, either as a more or less amorphous mass or as a spherical or oval structure which may have a thick wall.

Lest the description of the various modifications of cystidia prevent visualization of the typical form, the following characterization of a basidiomycetous cystidium is offered as a general statement. A hymenial cystidium is a sterile cell originating at the same general level and often in the same hyphal fascicle as the basidia and characteristically protruding beyond the apices of the basidia, usually hyaline but sometimes colored, either thin- or thick-walled and sometimes refractile, either lacking incrusting matter or covered with it over a part or all of its external surface, characteristically of larger size than basidia and cystidioles and usually of simpler form than dendrophyses and acanthophyses, its shape generally being cylindrical, fusiform, ovoid or conical. Brown cystidia must be distinguished from setae by criteria such as origin, shape, incrustation and reaction to treatment with potassium hydroxide solution.

The terms "pleurocystidium" and "cheilocystidium" have been used in the discussion of cystidial dimorphism. Buller (1922, p. 324) devised these words to describe the location on the lamella of the cystidia of agarics. Pleurocystidia grow from the two opposite faces of the lamella, while cheilocystidia originate from the edge. Sometimes the pleurocystidia and cheilocystidia of a lamella resemble each other; in other cases they are unlike one another or exhibit dimorphism. In addition to the two categories of lamellar cystidia, Buller (1924, p. 53) used the term "caulocystidium" for cystidia growing from the stipe and "pilocystidium" for those growing from the superior surface of the pileus. Although "pilocystidium" has been used by many authors (see Smith, 1947, p. 25 and Ainsworth and Bisby, 1950, p. 90), Lohwag (1941, p. 103) has substituted the word "pileocystidium". Both appear to be acceptable. Since the term "pilocystidium" might be construed as referring to the hairlike nature of the cystidium, not to its position upon the



cap surface, Lohwag's usage seems preferable. "Pleurocystidium" and "cheilocystidium" are usually restricted as terms applying to the gill fungi. They could, however, be used to refer to cystidia along the sides and tips of spines in the Hydnaceae or the sides and tips of the dissepiments in the Polyporaceae. They are not applicable to the Thelephoraceae or other groups with a smooth hymenial surface. The term "caulocystidium" is applicable to all cystidia borne on stipes, and the term "pileocystidium" is applicable to all cystidia borne on the superior surfaces, including those of species with simple pilei which lack gills, pores and spines.

Romagnesi (1944) takes exception to Buller's terms, particularly since he believes that they obscure the distinction between true cystidia and simple "hairs". He particularly objects to the use of "cheilocystidium", since the cystidiform elements on the gill edge often pass directly from the trama to the surface without showing differentiation and thus, by many mycologists, are believed not to be true cystidia. They are the "cystidiform hairs" of some authors, but the distinction between the so-called "hairs" and cystidia often is very obscure. Romagnesi has attempted to distinguish between the two by defining a cystidium as a sterile cell, morphologically and as a rule chemically differentiated, which is, basically, characteristic of the hymenium as marked by the presence of basidia; a "hair", on the other hand, is said to be a sterile cell, morphologically differentiated, which is, basically, characteristic of the sterile surface membrane. Romagnesi admits that there are exceptions to these definitions, as there are to nearly all generalizations. The fact is that Romagnesi's definitions may be reduced practically to the assertion that sterile modified elements accompanying the basidia are cystidia, while sterile modified elements borne on a surface lacking basidia are "hairs". It cannot be denied, however, that very often no morphological distinction can be made between these forms, and Buller's terms still appear to be applicable in nearly all instances. The cystidia appearing on sterile surfaces may be at least as distinctive and of as much value taxonomically as those borne in the hymenium. Corner (1950, p. 488), for example, has described long slender caulocystidia with one to five slender apical prolongations in *Pistillaria setipes* Grev., and also those of *Typhula graminum* Karst. (p. 670) which have bifid apices.

The exact position from which cystidia develop is important in determining whether there may be a homology of cystidia with basidia. De Bary (1873) claimed that cystidia have the same direction and seat as the basidia and are developed at nearly the same time as the basidia. Masee (1889, p. 119) admitted that some cystidia terminate lateral projections of the corymbose basidium-bearing branches. De Seynes (1873) believed that there is no fundamental difference between cystidia and basidia. He found that both originate at about the same level and that the hymenium seems to consist of hypertrophied basidia (cystidia), normal basidia and atrophied basidia ("paraphyses"). On the other hand, Boudier (1886) believed that cystidia should not be regarded as sterile basidia but as sterile branches of the subhymenial tissue, especially distinguished from basidia by their emergence from a lower stratum. Buller (1924, p. 271) found that the cystidia of *Coprinus atramentarius* (Fries) Fries arise at various depths beneath the hymenium from the outermost subhymenial cells to deep-seated subhymenial cells or even from the tramal cells. Lohwag (1926) reported that in the *Coprini* the cystidia occupy a position in the hymenium similar to that of the basidia. According to his belief, the cystidia are the structures formed first in the cyme-like basidial fascicle, the basidia are structures of the second order, and "paraphyses" structures of the third order in the fascicle. Corner (1932*b*), studying *Fomes levigatus* Corner, decided that the true cystidia arise, as do the basidia, from thin-walled, colorless, generative hyphae. He found that the terminal cell of the generative hypha enlarges into a basidium or a cystidium; then laterals from subterminal cells build up the hymenium by further sympodial branching.

Whelden (1936) studied the development of the basidia and cystidia in a fungus which he called *Peniophora livida* (Fries) Burt but which apparently was not that species. In his fungus the cystidia originate from hyphal tips which are distinguishable in no way from basidium initials. He was not able to distinguish a cystidium initial from that of a basidium until enlargement occurred. Corner (1947) has summarized the case for those who emphasize the basidium-like origin of the hymenial cystidia: "In spite of many attempts to classify and homologize cystidia, it is still generally overlooked that (1) cystidia are characteristically the first hymenial

elements to mature, being derived from the first hyphal endings in the primordial hymenium; (2) later-developed cystidia commonly have transitions to basidia with which in time and place of development they agree. It seems that cystidia represent sterile basidia which become overgrown without changing. I conclude that cystidia develop in the same way as the basidia but, through precocity or sterility, they become overgrown and much larger than the basidia".

As the hymenial cystidia originate at about the same level as the basidia, they occupy approximately the same position in the hymenium as the latter. Often, though, they are much more elongated than the basidia and thus protrude beyond the general level of the other hymenial elements. Often the protruding part is tapered, but sometimes the cystidium is cylindrical, or the protruding part may be actually of greater diameter than the hymenial part. The latter situation occurs in some species of *Coprinus*. Buller (1910; 1924, pp. 261, 300, 329) has described the large cystidia which, in some species of this genus, extend completely across the interlamellar space and sometimes are clasped at the apex by enlarged "paraphysis"-like structures which extend from the opposing lamella. According to Boedijn (1935), both the greatly enlarged cystidium and the clasping cells arise from the hymenium and therefore are to be designated as cystidioles. Bourdot and Galzin (1928, p. 168) have expressed the same criterion for determining a structure to be a cystidiole. While it probably is true that cystidioles usually originate in the subhymenium, not all structures originating at this level are to be considered cystidioles. Lohwag (1941, pp. 165-166) prefers to think of Boedijn's large cystidioles as hymenial cystidia and his small ones as enlarged "paraphyses". Probably it is somewhat preferable to retain the term "cystidioles" for the latter structures. Wettstein (1887) has summarized the relationships between sterile hymenial elements of opposing lamellae in the *Coprini*. In species such as *C. tomentosus* Fries, it is not unusual for the cystidia of neighboring lamellae to meet and fuse at their apices, but without disappearance of the apical wall. In some species the cystidia may elongate greatly and penetrate the trama of the opposing lamella, while in other species, as described above, the cystidia may be clasped at their apices by palisade-like cells of the opposing hymenium.

Nuclear activities in the hymenial cystidia could furnish a clue to the relationship of these cells to basidia. In the basidiomycetous sporocarp the non-reproductive cells of the secondary mycelium are binucleate, nuclear fusion characteristically being confined to the cell which eventually (directly or by a few further divisions as in some Heterobasidiomycetes) produces the basidiospores. If any other cell of the basidiocarp can be shown to have nuclear fusion, there appears to be no reason to deny its homology with the basidium. Generally one or the other of two nuclear conditions has been reported among the Basidiomycetes. The first of these involves the disintegration of the two nuclei of the cystidium without fusion occurring. Wager (1911) reported that in *Stropharia stercorearia* (Fries) Quél. and *Mycena galericulata* (Fries) Kummer, and possibly in other species, the cystidia appear to be developed from basidia in which the two nuclei do not fuse. He thought that in the process of glycogen formation in the cell the two nuclei gradually degenerate and disappear. The nuclear behavior reported here would not necessarily support the opinion that cystidia represent sterile basidia. Buller (1922, pp. 3-4) suggested that "paraphyses" and cystidia appear to differ from basidia in their nuclear behavior. He said that the "paraphyses" of *Coprinus porcellaneus* Schroet. [= *C. comatus* (Fries) S. F. Gray] differ from basidia by the failure of their nuclei to fuse, but he did not say how the cystidia of this species differ from the basidia. He goes on to say, though, that Ruhland failed to observe nuclear fusion in the large binucleate cystidia of *C. atramentarius*. There are several other references in the literature to the binucleate condition of cystidia. Some of these seem to imply that the two nuclei disintegrate without fusing. In other cases the implication is less clear. Practically all authors are in agreement that, at least when young, cystidia are binucleate, but Kühner (1926) reported a multi-nucleate condition of the cystidia in *Collybia tenacella* (Fries) Kummer. He thought there must be a binucleate young condition, but was unable to find it.

The second general nuclear condition reported for cystidia involves the fusion of the two original nuclei and sometimes indications of a reduction division. Maire (1902, p. 153) observed fusion of the original two nuclei to form a single fusion nucleus in cystidia of *Stropharia semiglobata* (Fries) Quél. Kühner (1925) observed nuclear fusion in cystidia of *Mycena fellea* Lange [= *M.*



*erubescens* Höhn.]. These cystidia were found to contain two nuclei which soon fuse to form a mass which is at first ellipsoidal and then rounded. The fusion nucleus has homogeneous-appearing nucleoplasm with two well separated nucleoli. The latter apparently remain separate. In most of the cystidia the fusion nucleus was found to rest without further change, but in a very few it was apparent that the nucleus undergoes division. At the apex of one cystidium a narrow transverse spindle and two centrosomes were observed, the division being at the stage of the equatorial plate and resembling very much the ordinary reduction division of the nuclei in basidia.

Whelden's (1936) study of the gloeocystidia and cystidia of his so-called *Peniophora livida* has been particularly useful in furnishing information about these structures. In many fungi the cystidia are thin-walled and not greatly different in their characteristics, other than shape and lack of spores, from the basidia. In "*P. livida*" the cystidia are very different from the basidia when mature, being much-elongated, more or less thick-walled cones which protrude 20 to 45 micra beyond the basidia. When very young they can not be distinguished from young basidia until after fusion of their two nuclei. Usually, after fusion, the nucleus becomes less and less distinct from the cytoplasm and finally disappears; at other times there is division of the fusion nucleus until there are recognizable eight distinct chromosomes which, except for their slightly larger size and often wider dispersal, are like those in the basidium. Whelden was not able to follow subsequent events very well, but often was able to find two relatively large and distinct nuclei which evidently had developed by the division of the fusion nucleus. He observed that these always disintegrate and disappear, so that a mature cystidium results. Greis (1937) found that the two nuclei in the cystidia of the lamella edge of *Lepiota acutesquamosa* (Weinm.) Kummer usually migrate to the apex of the cystidium and eventually disintegrate without fusing, but in some of the cystidia nuclear fusion may at least start, even though it may not be entirely carried through. An additional report of nuclear fusion in cystidia has been made by Ritchie (1940, 1941) who has observed it in cystidia of *Russula emetica* (Fries) Pers. ex S. F. Gray.

These observations by careful and reliable mycologists can leave no doubt concerning the reality of nuclear fusion in the cystidia of

at least some, and probably many, Basidiomycetes. There seems to be no logical conclusion other than that these cystidia are homologous with basidia. Before leaving this discussion of nuclei, attention should be directed to a slip of the pen made by Overholts (1929): "The function of cystidia has never been satisfactorily explained. Brefeld's view that they are metamorphosed basidia is borne out by the fact that they are said to contain, in young stages at least, the two nuclei characteristic of basidia." As has been explained, all cells of the secondary mycelium, which is the usual type of mycelium in basidiomycetous sporocarps, contain two nuclei. It is not the presence of two nuclei in the cystidium that is convincing evidence of its basidial nature, but the fact that nuclear fusion is known to occur.

Cystidia often are reputed to be of a more vacuolate nature than basidia, and this fact may be of help in distinguishing less conspicuous cystidia from young basidia (Kühner, 1925). On the other hand, Corner (1948a) has shown that basidia often are plentifully filled with vacuoles and that, at certain stages, these vacuoles may be exceedingly large so that they fill practically the entire basidium. Thus there seems to be no real distinction between cystidia and basidia in this respect. Corner believes that the vacuoles of basidia may have the very important role of pushing the protoplasm from the basidium into the developing spores, so that the basidium at last is almost entirely empty of protoplasm.

De Bary (1873) and Buller (1924, pp. 348-350) studied the cystidia of *Coprinus micaceus* (Fries) Fries. They found that there is a central mass of cytoplasm formed where numerous thin plates of cytoplasm meet at the center of the cell. De Bary spoke of these plates as filiform and branching processes, but Buller believed that they are formed in plates, similar to the walls of foam bubbles, and that the central mass slowly changes form and position by alterations in the relative volumes of the vacuoles enclosed by the numerous thin cytoplasmic walls. In older cells the cytoplasm may be limited to the periphery of the cell, with one huge vacuole occupying the cell center. This is similar to the final stage of vacuole formation in some basidia, as described by Corner. Buller (1924, p. 107) found similar cytoplasmic plates separating vacuoles in the cystidia of *Pluteus cervinus* (Secr.) Kummer. In *Coprinus atramentarius* (Fries) Fries (Buller, 1910; 1924, p. 275) the

young cystidium is provided with a large amount of cytoplasm, but the full-grown cell contains a small accumulation of cytoplasm at each end, a very thin cytoplasmic layer lining the cell wall, and a large central vacuole filled with clear and colorless cell sap. Buller found that the turgidity of these cystidia maintains their rigidity, since they collapse when killed.

In the cystidia of "*Peniophora livida*" (Whelden, 1936) the cytoplasm at first is coarsely vacuolate throughout. It becomes increasingly vacuolate, and a large vacuole forms in the basal part. The cell nucleus becomes progressively less distinct from the cytoplasm surrounding it until finally it is unrecognizable. Kühner (1925) was able to see a fine cytoplasmic network in fixed and stained cystidia of *Mycena fellea* [= *M. erubescens*]. There were also many refractile droplets which did not color when treated with osmic acid and thus were not of an oily nature.

Locquin (1945) has described an interesting process of endo-vacuolar formation in pleurocystidia of *Pluteus umbrosus* (Fries) Kummer sensu Ricken. The majority of these cystidia have their vacuole divided in two by a horizontal protoplasmic "bridge". Later the protoplasmic bridge invaginates toward the base of the cystidium, and the apical vacuole enters this invagination. The invagination finally is closed by the meeting of the two lateral wings of the bridge, and the protoplasmic wall enclosing the small vacuole breaks its attachment with the protoplasmic layer lining the cystidial wall. The vacuolar inclusion finally has the form of a colorless and refractile sphere which includes a brown, spherical, homogeneous vacuole. The entire structure lies in the middle of a large vacuole occupying nearly the entire cystidium. In certain cases two or more of these vacuolar formations may coexist, superimposed one above the other. The refractile corpuscles which Romagnesi (1944) has observed in cystidia of *Nematoloma* mounted in ammonia seem to have some similarity to these vacuolar inclusions described by Locquin.

Patouillard (1882) has called attention to the fact that crystals or amorphous masses of calcium oxalate may appear in various parts of the basidiocarp but are to be sought mainly in the parts less immediately concerned with reproduction. They are not associated with organs of reproduction except when these are sterile. He has directed attention to the presence of calcium oxalate crystals on the

cystidial walls of *Pleurotus ostreatus* (Fries) Kummer, *Peniophora sambuci* (Pers.) Burt and *Polyporus abietinus* Fries and the absence of crystals on the basidia of these species. The presence of these crystals caused Patouillard to believe that cystidia may be excretory elements.

Topin (1901, pp. 58-60) studied a large number of Hymenomycetes and found crystalline matter on the cystidial walls of 59 species. In all instances where these incrustations could be identified, they consisted of calcium oxalate. Romagnesi (1944) has summarized the various substances which have been reported to be excreted by cystidia. These include water, mucilages, mineral salts, particularly calcium oxalate, resinous materials, fatty substances and various colored substances of unknown chemical nature.

Cystidial incrustations are of diverse forms, depending mainly on the species in which they occur. Many species of *Peniophora*, *Stereum* and other genera have cystidia which have their entire free surface covered by a more or less amorphous envelope of refractile matter. In *Inocybe* and some other genera the apex of the cystidium may be crowned by acicular crystals. Other genera may have species which bear caps or collars of mucilaginous substances, as is true of several species of *Mycena*. Buller (1922, p. 325) has described the formation of mucilage drops at the apices of cheilocystidia in *Panaeolus campanulatus* (Fries) Quél. Such drops tend to be plano-convex, apparently because they are unable to pass from the tips down the shafts of the cystidia. Drops from adjoining cystidia may coalesce to form large drops as broad as one-tenth millimeter.

Boudier (1890) suggested that it is not necessary to think of cystidia as special excretory elements to account for the external deposits which appear on them so often. He believed that any filament in an active state of growth might have these substances and that they are deposited on the exterior of the cell wall by exosmosis. More recently the majority of mycologists seem to have accepted Patouillard's characterization of these structures as special excretory elements. Knoll (1912) has been particularly interested in the hydathode nature which he believed cystidia to have. He found that cystidia of this nature have the following characteristics: (1) The secretion of liquid is limited to a sharply circumscribed area at the tip of the cystidium; (2) the place where liquid is



secreted is thin-walled; (3) the drops of liquid contain a colloidal substance derived from the cystidial wall as the result of a strong local mucilagination. The cystidia of *Psathyrella consimilis* Bres. & P. Henn. [= *P. pygmaea* (Quél.) Sing.] illustrate these principles. There is formation of a mucilage cap at the cystidial apex, with the crystals then being formed at the boundary between the mucilage and the membrane of the cystidium. Thick-walled cystidia of species such as *Peniophora glebulosa* (Fries) Sacc. & Syd. may have thin-walled apices. The thin-walled apex of such a cystidium often is covered by a mucilaginous sheath and abundant crystalline matter. To Knoll this signified the hydathode nature of these cystidia. In *Inocybe petiginosa* (Fries) Gill., Knoll found that the wall of the cystidial apex is thickened greatly and has a cuticle-like outer membrane. Investigation of alcoholic preparations seemed to show that only the middle layer of the thickened cell wall is mucilaginized. This mucilage formation causes the outer membrane to be raised up and eventually to burst. Knoll could not determine how much of this condition was caused by action of the alcohol. Corner (1950, p. 19) has described a similar situation in the oleocystidia of *Physalacria* and *Hormomitaria*. These have an oily resinous apical exudation. The exudation is inter-lamellar, being covered by the thin outer layer of the cystidium wall. Heim (1931, p. 40) found that cystidia in various species of *Inocybe* eliminate colorless or slightly colored substances as colloidal oily globules and as mineral elements, of which the principal kind is calcium oxalate. The latter are deposited on the exterior surface of the cystidial apex after the liquid material has passed through the membrane. Heim found that the cell wall may be composed of an exterior primordial membrane and an internal incrustated membrane constituted by layers of concreted material successively deposited on the primary membrane from the substance inside the cell. Levine (1913) laid much more stress than Knoll on the gelatinous property of the drops of liquid at the cystidial apex. He held cystidia of the *Boleti* to be glands similar to the glands of higher plants. Kallenbach (1926) likewise emphasized that the droplet formation at the cystidial apex is not a matter of excreting pure water but of eliminating substances which are to be regarded as end-products of fungus metabolism.

Some cystidia have finger-like diverticules protruding from the surface. These have been likened to the sterigmata of basidia by

some mycologists, but Heim (1931, p. 39) says that they really are excretory in nature and thus are not to be compared with sterigmata. Kühner (1938, p. 82) has noted that these diverticules often are capped with mucilage and thus resemble the cystidial apex on a much smaller scale.

In summary, it should be emphasized that hymenial cystidia originate at the same general level as the basidia. Their position and nuclear condition, and occasionally their form, suggest that they are sterile hypertrophied basidia. They sometimes have crystalline or amorphous matter covering their walls, and this suggests that they may be excretory cells. The suggestion has been made (Tieghem, de Bary, Buller) that cystidia are nothing more than prominent hymenial hairs. Kühner (1925) has discussed this matter and rejects any analogy between cystidia and hair-like formations such as paraphyses of Ascomycetes.

It has been suggested that cystidia may be useful to the basidiocarp in various ways. The pointed shape of many cystidia suggests that they may afford some protection to the hymenium against forays by slugs and other small animals. Massee (1906, p. 48) called attention to the fact that a number of mycologists have felt this to be a possibility. Buller (1909, p. 18) thought that the pointed cystidia of *Peniophora* could afford some protection to the hymenial elements of various species in this genus. Later (1922, p. 219; 1924, pp. 110-111) he reported that basidiocarps of *Pluteus cervinus* (Secr.) Kummer; *Inocybe rimosa* (Fries) Kummer and *Coprinus micaceus* (Fries) Fries all are eaten by slugs, even though they have numerous cystidia, and he saw that a slug (*Limax maximus*?) was able to eat probably thousands of the hook-tipped cystidia of *Pluteus cervinus* (Secr.) Kummer without obvious harm.

The cystidia of broad-gilled agarics serve a very obvious function, one that has been reported often. More than 200 years ago Micheli (1729) suggested that cystidia of the type found in some species of *Coprinus* might assist in the dispersal of spores by helping to keep the gills separated. Brefeld (1877, p. 57) suggested this function for cystidia of *C. stercorarius* Fries, and Copeland (1904) reported a similar situation in *C. fuscusporus* Copeland. These species have numerous broad moist gills that probably would stick together if the cystidia did not keep them apart. Buller (1924,

pp. 270, 322, 342) reported that a number of species have cystidia of this nature. In *C. atramentarius* (Fries) Fries (Buller, 1910; 1924, pp. 270-275) the cystidia stretch across the interlamellar spaces, thus holding the gills apart. Their apices are clasped and held by enlarged cystidioles borne on the opposing lamella. Each cystidium undergoes autodigestion a few minutes before the basidia in its vicinity discharge their spores; thus the cystidia do not obstruct the spore fall. The zone of cystidial autodigestion and spore discharge progresses gradually upward from the lamella edge to its base. In *C. lagopus* (Fries) Fries (Buller, 1924, pp. 322-325) the cystidia act as stays to hold the lamellae apart during spore formation, but later the gills separate widely and the cystidia merely project like pegs into the interlamellar spaces. In *C. micaceus* (Buller, 1924, p. 342) some of the cystidia may serve as stays, but many are never called upon for this purpose and merely act as guards which protrude into the interlamellar spaces. Cystidia of other species may project similarly across or into the interlamellar spaces. The pleurocystidia of *C. plicatilis* (Fries) Fries (Buller, 1931, p. 45) stretch almost or completely across the interlamellar spaces, but their apices are not united with the cystidioles of the opposing gill, so they do not lock adjacent gills together as do those of *C. atramentarius* and *C. lagopus*. Where cystidia protrude from the swollen edges of gills (cheilocystidia), Buller (1909, p. 17) regards them as packing cells. Cystidia of this type are found in *C. comatus* (Fries) S. F. Gray and in *Lepiota cepaestipes* (Fries) Kummer [= *Leucocoprinus cepaestipes* (Fries) Pat.]. Buller (1924, p. 21) says that cheilocystidia may be regarded as specialized hymenial cells simply filling up a space that can not be used satisfactorily for the production of spores.

#### CYSTIDIOLES, BASIDIOLES, PARAPHYSES, PSEUDOPHYSES

Cystidioles probably are much more numerous in basidiomycetous hymenia than references to them would indicate. Very often they are described as "cystidia" or "paraphyses", or are entirely ignored. Bourdot and Galzin (1928, p. 168) have reported cystidioles in a number of species of *Corticium*, including *C. serum* (Pers.) Fries [= *Peniophora sambuci* (Pers.) Burt], *C. laeve* (Fries) Fries, *C. harioti* Bres., *C. ochraceofulvum* Bourd. & Galz. and *C. expallens* Bres. According to Rogers and Jackson (1943),

*C. subpallidulum* Litsch. has highly characteristic capitate cystidioles. Pilát (1936) reported both cystidia and cystidioles in *Mycoleptodon fuscoatrum* (Fries) Pilát, and Singer (1926) found cystidiole-like structures in several species of *Russula*. Corner (1950, pp. 19-20) reports that many so-called cystidia in the clavarioid fungi actually are cystidioles. He mentions species of *Pterula*, *Clavaria* and *Caripia* [= *Podostrombium*] as well as perhaps *Pistillaria*, *Ramaria* and *Clavulinopsis*.

Cystidioles usually are thin-walled, non-incrusted, sterile hymenial elements, either pointed or obtuse at the apex, of approximately the same diameter as the basidia, arising at approximately the same level as the basidia, and usually protruding only slightly beyond the hymenial surface, although in some species they may protrude a considerable distance. They are not juvenile cystidia, nor are they immature basidia, but probably represent the simplest form of distinctly modified, permanently sterile basidium.

While most cystidioles are distinctive only because they protrude somewhat beyond the hymenial surface, various species of Basidiomycetes have been found to have hymenial elements which must be classed as cystidioles, even though they have very unusual form. Elements of this nature have been reported, for example, by Zeller and Walker (1935) and by Martin (1938). The former studied *Gasterella lutophila* Zeller & Walker. The spore of this species is broadly citriform, with a dark brown epispore which is uniformly verrucose except at the apiculus. Most basidia of this species bear four spores on well-developed sterigmata. In addition to these normal basidia, however, there may be found occasional basidium-like elements which bear no sterigmata, but each of which is capped by a single globose, dark brown, uniformly verrucose structure much resembling an enlarged spore. This head, seated directly on the basal basidium-like part of the element, is not abstricted and must be regarded as an integral part of the structure. The element is a modified basidium and may be regarded as a cystidiole. Martin found a similar occurrence in *Myxomycidium flavum* Martin. This species has a particular kind of hymenial element, apparently a modified basidium, which bears a vesiculose swelling at its apex. In some instances the basidium-like part of the element has apical processes, appearing to be modified sterigmata, which clasp the terminal vesicle. These elements are distinct from the ordinary basidia and appear to be cystidioles.



Basidioles are similar to cystidioles in some respects, since they represent sterile basidia, but they do not exceed the dimensions of mature basidia, do not protrude beyond the general hymenial level, and many basidioles later develop into mature sterigmate basidia. In other words, basidioles are young basidia or basidia in which growth has been arrested before production of sterigmata. In the very young hymenium all the basidia might be termed "basidioles". Filiform basidioles of some species, such as *Stereum fasciatum* (Schw.) Fries, may bear a few short apical diverticules. Such elements may be termed "aculeate basidioles" but are actually small sparsely pronged acanthophyses. Basidioles have been described and discussed for several Gasteromycetes but have been called "primary basidia" or "cystidia". Walker (1927) has studied the "primary basidia" which appear during development of the gleba in *Sphaerobolus iowensis* Walker and *S. stellatus* Tode. They are enlarged hyphal ends with scanty protoplasm that appear at a particular stage preceding spore formation. Lohwag (1941, pp. 181-183) believes that these elements, and similar structures reported in other species such as *Leucogaster floccosus* Hesse and *Geastrum velutinum* Morg., are space makers which later disappear to make room for the spore-bearing basidia. The fact that these elements undergo nuclear fusion with development of a double spireme shows that they are immature precocious basidia and thus are basidioles.

Use of the terms "basidiole" and "cystidiole" leaves little room for another term that appears frequently in the literature concerning Basidiomycetes. The latter term is "paraphysis". In the Ascomycetes this refers to a uninucleate haploid element intercalated among asci which have arisen from a binucleate cell. In the Homobasidiomycetes the "paraphysis" is a binucleate cell and often is merely a young basidium. "Basidiole" therefore is more applicable to structures of this type appearing among the Hymenomycetes, and "paraphysis" is a misnomer.

"Paraphysis" also has been used as a loose generic designation for the various kinds of nodulose, pronged or branched hyphal ends which appear in the hymenia of some species. The simplest form of these structures is found in the "pseudophyses" which Höhnelt and Litschauer (1907) distinguished in *Aleurodiscus*. These are thin-walled unbranched hymenial structures which are more or less cylindrical but which may be constricted at frequent intervals, par-

ticularly toward the apex, so that they are moniliform, somewhat like a very short string of beads. The term "pseudoparaphyses" has been used for the short, broad, thin-walled cells which separate the basidia in species of *Coprinus*, *Bolbitius* and *Drosophila* (see Romagnesi, 1944; also Langeron, 1945, pp. 82, 323-324). These may be regarded as basidioles.

#### ACANTHOPHYSES AND DENDROPHYSES

Acanthophyses and dendrophyses are more elaborate structures than the preceding, but often have been termed "paraphyses". Of course they have not the slightest relationship with true paraphyses. Originally the bottle-brush forms were called "dendrophyses" (Höhnelt and Litschauer, 1907); then both the bottle-brush and dendroid forms were included under that term. Pilát (1926) later introduced the term "acanthophysis" for the bottle-brush form, and subsequently the bottle-brush forms have been referred to by that term, while the dendroid forms are still called "dendrophyses".

Acanthophyses are especially prominent in certain species of *Aleurodiscus*, including *A. cerussatus* Bres., *A. farlowii* Burt, *A. cremeus* Burt and *A. tenuis* Burt. Other species of *Aleurodiscus* also have such structures, but in some, as *A. oakesii* (Berk. & Curt.) Cke., the prongs may be few and may occur only at the base, only along the central part or only at the tip of the acanthophysis. Acanthophyses also are found in some species of *Stereum*, particularly in *S. frustulatum* (Fries) Fckl. and related species. The aculeate basidioles of certain species of *Stereum*, as *S. fasciatum*, are really small acanthophyses which have only a few prongs at the apex. According to Bourdot and Galzin (1928, p. 376), the abundance of acanthophyses in the hymenium, at least in some species, is inversely proportional to the activity of the hymenium. Singer (1945) has discussed the acanthophyses of *Favolaschia*, although he refers to them as "dendrophyses", evidently in accordance with the earlier terminology of Höhnelt and Litschauer. He also seems to include the unbranched, smooth, cylindrical or nodulose structures commonly known as "pseudophyses" in his concept of dendrophyses. He says that the latter structures are found both in the hymenium of some species of *Aleurodiscus* and on the outside of the cups of *Cyphella*. He traces possible relationships among several genera, including *Cyphella*, *Aleurodiscus* and *Favolaschia*,

depending to some degree on the similarity of sterile elements in these genera.

Dendrophyses have been observed in species of several genera, including *Sebacina*, *Tremellodendron*, *Aleurodiscus*, *Stereum* and *Peniophora*. Probably they represent several types of structures, some of which are strictly hymenial elements and others of which are found also in the context. All are characterized by their irregular or dendroid branching. Some may have only a few branches, while others have a great number which, in turn, may be repeatedly branched. They may be either hyaline or colored. Those of *Stereum versiforme* Berk. & Curt. originate from the context and are a grayish-brown color. They may bear occasional clamp connections where they originate in the context, but lack clamp connections in the hymenium. According to Lohwag (1941, p. 39) the sparsely branched structures in species of *Sebacina* may be homologous with the basidia, and the acanthophyses of some species of *Aleurodiscus* may be of a similar nature. Wittlake (1938) found that the branched or unbranched structures in the hymenium of *Sebacina calcea* (Pers.) Bres. may originate from the same hyphae which bear the basidia, and may bear clamp connections. Some were found to proliferate from the apices of probasidia and to form a stout apical structure having several branches. Whether these elements should be called "dendrophyses" is open to question. Actually they are more or less similar to the much-branched septate hyphal ends with clamp connections that appear in the hymenium of *Stereum roseo-carneum* (Schw.) Fries. Burt refers to these as branched "paraphyses" and fails to note the clamp connections.

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## GLOSSARY

ACANTHOPHYSIS (BOTTLE-BRUSH PARAPHYSIS): A sterile hymenial hyphal end that has a number of tine-like diverticules protruding from the surface.

ASTEROPHYSIS: See STELLATE SETA.

BASIDIOCARP: A sporocarp that bears basidia and basidiospores. (See also SPOROCARP, HYMENOPHORE, FRUITING BODY).

BASIDIOLE: A basidium-like hymenial element that lacks sterigmata either because it is young or because it is permanently sterile. (See also PARAPHYSIS, PRIMARY BASIDIUM, CYSTIDIOLE).

BOTTLE-BRUSH PARAPHYSIS: See ACANTHOPHYSIS.

CAULOCYSTIDIUM: A cystidium borne on the stipe of a basidiocarp.

CHEILOCYSTIDIUM: A cystidium borne on the edge, not on the faces, of a lamella.

CONTEXT: The hyphal mass occupying the region between the superior surface and the subhymenium in basidiocarps lacking lamellae, pores or spines, and also the similar mass in the cap but not in the lamellae, pores or spines of basidiocarps having the latter structures. (See also TRAMA).

CYSTIDIOLE: A simple hymenial cell of approximately the same diameter as the basidium but remaining sterile and protruding beyond the hymenial surface. (See also PARAPHYSIS, BASIDIOLE).

CYSTIDIUM: An enlarged, conical, prismatic or cylindrical sterile end of a non-vascular hypha, characteristically hyaline or pale-colored but sometimes brown and distinguished then from a seta by origin, form or failure to darken in potassium hydroxide solution, borne usually in the hymenium but sometimes remaining submerged or appearing at other surfaces of the basidiocarp. (See also PLEUROCYSTIDIUM, CHEILOCYSTIDIUM, PILEOCYSTIDIUM, CAULOCYSTIDIUM, HYMENIAL CYSTIDIUM, TRAMAL CYSTIDIUM, LAMPROCYSTIDIUM, LEPTOCYSTIDIUM, METULOID, PSEUDOCYSTIDIUM, GLOEOCYSTIDIUM, CYSTIDIOLE, BASIDIOLE, PRIMARY BASIDIUM).

DENDROPHYSIS: A sterile hyphal end in the context or hymenium characterized by irregular tree-like branching.

DERMATOGLOEOCYSTIDIUM: See PILEOGLOEOCYSTIDIUM.

DICHOPHYSIS: A sterile hyphal end in the context or hymenium, characterized by rigid regularly dichotomous branching.

**EMBEDDED SETA:** An enlarged, elongated, brown, thick-walled tube embedded in the context or trama of a xanthochroic basidiocarp and generally following the course of the ordinary hyphae of the region in which it occurs. (See also **SETA**).

**FACIAL CYSTIDIUM:** See **PLEUROCYSTIDIUM**.

**FALSE SETA:** A seta-like end of a skeletal hypha extending into or beyond the hymenium.

**FRUITING BODY:** See **SPOROCARP**.

**GLOEOCYSTIDIUM:** A sterile hyphal end considerably modified for either a short or a relatively long distance from the apex so that it is broader than the hypha from which it originates, thin-walled, characteristically non-septate, usually of irregular form, often long and tortuous with the base broader than the apex, usually bearing highly refractile hyaline or yellowish contents, originating in the context, trama or subhymenium as a rule, and seldom protruding beyond the hymenial surface. (See also **PILEOGLOEOCYSTIDIUM**, **PSEUDOCYSTIDIUM**, **TRAMAL CYSTIDIUM**).

**HYMENIAL CYSTIDIUM:** A cystidium originating at approximately the same level as the basidia and often arising directly from the basidial fascicle. (See also **TRAMAL CYSTIDIUM**).

**HYMENIAL SETA:** A seta borne in the hymenium.

**HYMENOPHORE:** A sporocarp that bears an hymenium. (See also **SPOROCARP**, **BASIDIOCARP**).

**HYPHAL END:** The apical extremity of a hypha together with a short adjacent part of indefinite length.

**HYPHAL PEG:** A tuft of hyphae originating in the context or adjacent subhymenium and passing through the hymenium and protruding beyond it as a sterile hyphal column.

**HYPHAL SERIES:** Those hyphae of a basidiocarp that have a particular kind of anatomy in common and all of which bear a particular relationship to the other hyphae of the basidiocarp. Three series have been described: the generative series, the skeletal series, and the binding series. (See also **HYPHAL SYSTEM**).

**HYPHAL SYSTEM:** The sum of the hyphal series in a basidiocarp. The hyphal system is said to be "monomitic" when all of the hyphae of the basidiocarp are of the generative series; when the generative and skeletal series are present, the system is



"dimitic"; when the generative, skeletal and binding series all are present, the system is "trimitic". (See also HYPHAL SERIES).

LAMPROCYSTIDIUM: A cystidium that has a thick, refractile wall. (See also LEPTOCYSTIDIUM).

LATEX HYPHA: See LATICIFEROUS HYPHA.

LATICIFEROUS HYPHA: A vascular hypha that contains a milky liquid, either white or variously colored, believed to be a latex.

LEPTOCYSTIDIUM: A thin-walled cystidium larger than a cystidiole. (See also LAMPROCYSTIDIUM).

METULOID: An incrusted, more or less spindle-shaped cystidium of the type found in several species of *Stereum* and *Peniophora* as well as in various other genera.

PARAPHYSIS: A sterile hyphal end that often accompanies the ascus in the hymenium of the ascocarp but which never has conjugate or diploid nuclei. The so-called "paraphysis" of the basidiocarp is more closely akin to the basidium than the true paraphysis is to the ascus and preferably is called a "basidiole" or "cystidiole". (See also CYSTIDIOLE, BASIDIOLE).

PILEOCYSTIDIUM (PILOCYSTIDIUM): A cystidium borne at the superior surface of the basidiocarp.

PILEOGLOEOCYSTIDIUM (DERMATOGLOEOCYSTIDIUM): A gloeocystidium-like structure borne at the superior surface of the basidiocarp.

PILEOSETA: A seta borne at the superior surface of the basidiocarp.

PLEUROCYSTIDIUM (FACIAL CYSTIDIUM): A cystidium borne on the face or side, not on the edge, of a lamella.

PRIMARY BASIDIUM: A basidiole which precedes the development of the mature hymenium and acts as a space-making structure in the developing gleba of various Gasteromycetes.

PSEUDOCYSTIDIUM: The hymenial end of a vascular hypha. (See also TRAMAL CYSTIDIUM, GLOEOCYSTIDIUM, FALSE SETA).

PSEUDOPARAPHYSIS: A short, broad, thin-walled basidiole in *Coprinus*.

PSEUDOPHYSIS: A filiform, often moniliform, basidiole in *Aleurodiscus*.

SANGUINOLENTOUS HYPHA (TANNIC ACID HYPHA): A thick-walled vascular hypha that contains a liquid or solid reddish-brown material reputed to be tannic acid, and also a vascular hypha

lacking the reddish-brown material but homologous in structure with the liquid-containing hypha.

**SAP HYPHA:** A vascular hypha that contains a conspicuous liquid material.

**SETA:** A brown, spine-like, sterile hyphal end appearing in various parts of xanthochroic basidiocarps. It never is very conspicuously incrustated, usually is thick-walled and darkens conspicuously when moistened with potassium hydroxide solution. (See also **HYMENIAL SETA**, **EMBEDDED SETA**, **PILEOSETA**, **STELLATE SETA**, **FALSE SETA**).

**SPHAEROCYST:** A greatly enlarged pellucid cell situated among the ordinary hyphae in *Lactarius* and *Russula*. In the stipe such cells often are somewhat elongated in a direction parallel with the axis of the stipe and frequently are seen to be arranged in a rosette-like group when the stipe is examined in transverse section. In the cap they are more nearly globose and are more irregularly disposed.

**SPOROCARP:** The entire multi-cellular hyphal association, usually in the form of a prosenchymatous to pseudoparenchymatous body, that bears spores. (See also **BASIDIOCARP**, **HYMENOPHORE**).

**STELLATE SETA (ASTEROPHYSIS):** A compound seta having several radiating arms mostly situated in a plane parallel with the hymenial surface.

**TANNIC ACID HYPHA:** See **SANGUINOLENTOUS HYPHA**.

**TRAMA:** The relatively unspecialized layer of hyphae occupying the central part of the lamella, the spine or the dissepiment between pores in the Agaricaceae, the Hydnaceae and the Polyporaceae, respectively. The trama is bordered by the subhymenium along the sides and by the context above. (See also **CONTEXT**).

**TRAMAL CYSTIDIUM:** A cystidium that originates from the context or trama instead of the hymenial region. See also **HYMENIAL CYSTIDIUM**, **PSEUDOCYSTIDIUM**, **GLOEOCYSTIDIUM**, **FALSE SETA**).

**TRICHODERM:** A layer of long, slender, more or less parallel, erect, hairlike hyphae which originates from the superior surface of the basidiocarp.

**VASCULAR HYPHA:** A tube-like hypha that is non-septate or sparingly septate and which also is conspicuous because of its large diameter or distinctive contents or both.

**VESICULAR BODY:** An inflated, pyriform to subglobose, bladder-like sterile hyphal end that usually is situated in the context or trama, or more rarely in the hymenium. It may bear hyaline or yellowish and refractile contents, or may appear empty.

**XANTHOCHROIC FRUITING BODY:** A basidiocarp having the hyphae of the context and trama yellowish-brown when observed in a water or acid mount, but dark brown when moistened with potassium hydroxide solution.

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